

AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024
Number 3109, 53 pp., 18 figures, 1 table

November 8, 1994

Identifying Isolated Shark Teeth of the Genus *Carcharhinus* to Species: Relevance for Tracking Phyletic Change Through the Fossil Record

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ABSTRACT

Most sharks can be identified to genus on the basis of a combination of their tooth shapes and tooth counts. Some sharks can even be identified to species by this means. The requiem sharks (genus *Carcharhinus*) are one such group. This group also has a dense and relatively continuous fossil record of isolated teeth extending from the Eocene to the present day. If a means could be developed to identify their isolated teeth to species, it would be possible to trace directly their evolutionary history through the fossil record. This would provide an unprecedented opportunity to investigate the tempo and mode of evolutionary change.

In this study we investigated the extent to which the isolated teeth of extant *Carcharhinus* can be correctly assigned to species using discriminant function analysis of linear measurements. We measured 12,647 extant teeth representing shape

variation due to species, ontogeny, sexual dimorphism, jaw, and tooth position. Observations were split into a "training" data set used to establish the discriminant functions and a "test" data set used to evaluate their efficiency. We found that excellent discrimination could be achieved for teeth from certain parts of the dentition. Results indicate that teeth from the upper jaw are correctly assigned to species more often than are teeth from the lower jaw and that teeth from central positions within a tooth series (half-way between the symphysis and the angle of the jaw) are correctly assigned to species more often than are teeth from other positions. Quadratic discriminant analysis was used to assess whether or not the jaw and tooth positions of isolated *Carcharhinus* teeth could be determined. While classification accuracy varied across species, results indicate that upper jaw teeth

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can be readily distinguished from lower jaw teeth and that "maximally distinctive teeth" can be distinguished from teeth at less distinctive positions within the jaw. These findings are used to propose

an objective and quantitative protocol for the interpretation of phyletic change in fossil *Carcharhinus* teeth.

INTRODUCTION

The requiem sharks of the genus *Carcharhinus*, family Carcharhinidae, are represented by 30 living species that range across tropical, subtropical, and temperate waters of the world. These are the dominant sharks in tropical waters, both in variety and in biomass (Compagno, 1984). All species of *Carcharhinus* are found in coastal waters with the exception of two, the Oceanic White-tip Shark (*C. longimanus*) and the Silky Shark (*C. falciformis*) both of which are oceanic, inhabiting ocean basins hundreds of miles off shore. One species, the Bull Shark (*C. leucas*) is tolerant of both coastal marine and freshwater environments and moves freely between the two. All members of the genus are voracious predators, feeding primarily on rays, other sharks, teleosts, molluscs and crustaceans (Compagno, 1984). Species within *Carcharhinus* range in total length from about 80 cm to approximately 4 m. Some of the larger species are known to have attacked swimmers and are among the most dangerous of living sharks (Compagno, 1984).

Most species of *Carcharhinus* are similar in body form (Garrick, 1982; Compagno, 1984) and most are light gray in color. A few have distinctive markings which, when present, are almost exclusively restricted to the fins. The relative similarity of body form among different species often makes field identification difficult. In such situations it is usually fin placement, fin shape, and fin markings that enable positive identifications to be made.

While overall body form varies little across species within *Carcharhinus*, dentition, by contrast, is highly species specific. A typical *Carcharhinus* dentition can be seen in figure 1. The jaw apparatus comprises two paired cartilages, the upper jaw being formed by the palatoquadrate, the lower jaw by Meckel's cartilages. Each section of cartilage has teeth on its occlusal margin. The number and shape of these teeth (see fig. 2) is often the most reliable quick way to distinguish between cer-

tain species in the field (Naylor, personal obs.). Garrick (1982) has also noted the utility of tooth shape for species identification in *Carcharhinus*, and has singled out the shape of the fifth upper jaw tooth (the fifth tooth from the central symphysis) as being particularly distinctive for species identification.

Teeth in *Carcharhinus*, as in all sharks, are replaced continuously throughout life. Those at the outer margin of the jaw are replaced, as if on a conveyor belt, by new teeth forming on the inner margin (figs. 3, 4). A typical *Carcharhinus* will have approximately 250 teeth in its jaw at any given time (fig. 3), the outermost 50 of which will be fully formed, erect, and functional, the remaining 200 comprising replacement teeth at various stages of development. The replacement process is prolific. Individual sharks of some modern species are estimated to loose thousands of teeth in a lifetime (Moss, 1967). In the past, a number of these teeth have become fossilized in marine coastal sediments, and constitute the most dense and continuous record of any vertebrate in the entire fossil record (Maisey, 1984).

If fossil sharks of the genus *Carcharhinus* are identifiable to species from the shape of their teeth, in the same way that living forms seem to be, then it should be possible to trace lineages of *Carcharhinus* species through the fossil record at successive geological horizons (Naylor, 1990).

Unfortunately, this proves to be more difficult than it might appear at first, because there is a smooth tooth shape gradient extending along a tooth series from the symphysis to the angle of the jaw within individual sharks (see fig. 2). It is as though the incisors, canines, premolars, and molars of mammals smoothly graded into one another such that they were no longer discretely recognizable. This smooth gradient confounds the identification of homologous teeth across species and, in so doing, blurs the species-specific distinctiveness in tooth shape that

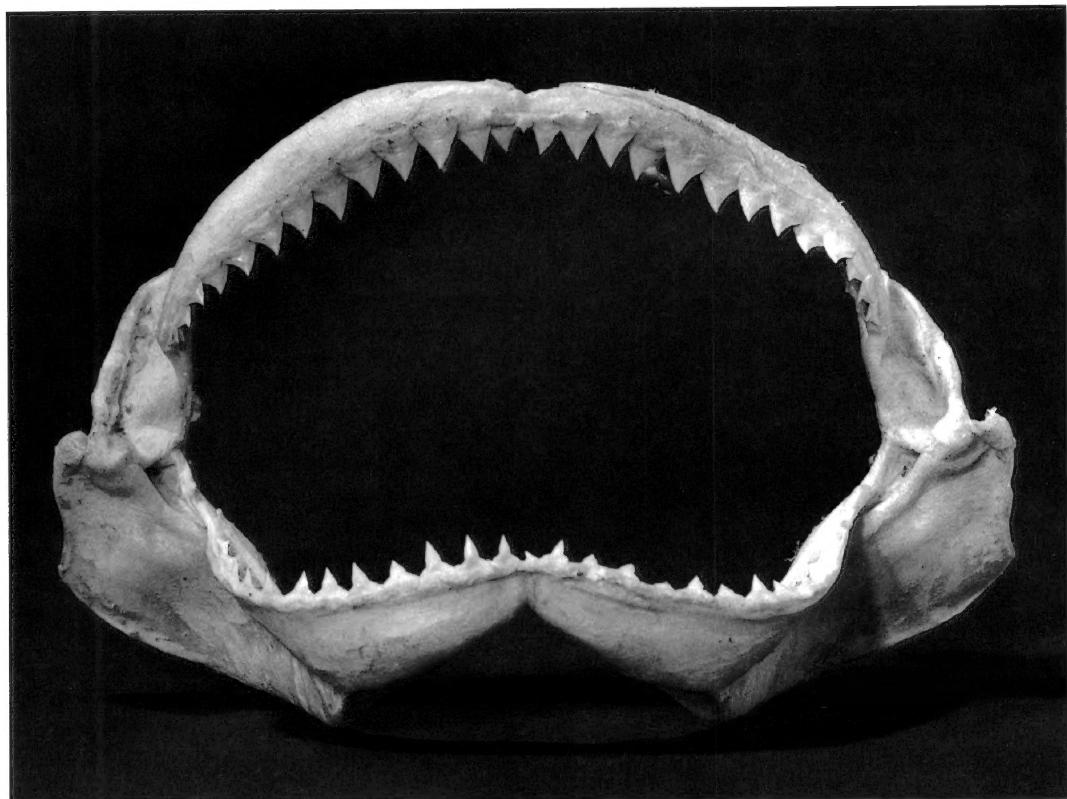


Fig. 1. Bull Shark (*Carcharhinus leucas*) jaw viewed from front, showing upper and lower jaw dentitions. The entire jaw comprises four cartilaginous elements: the paired palatoquadrate forming the upper jaw and the paired Meckel's cartilages forming the lower jaw.

might otherwise be detected if purely homologous comparisons could be ensured. The difficulty is further exacerbated in the case of the isolated shark teeth found in the fossil record because their original tooth position placements around the jaw, within a tooth series, are not immediately determinable.

Paleontologists working with the fossil record of isolated shark teeth are thus faced with a tantalizing problem: They can collect large samples of fossil teeth, from one of the most continuously represented vertebrate groups in the fossil record. A number of these fossil teeth (those originating from certain regions of the jaw) are considered to be distinctive enough to permit species identification. However, they cannot objectively distinguish these "informative teeth" from similarly shaped teeth that come from less informative parts of the jaw. As a result, studies designed to investigate phyletic change through the fossil shark-tooth record tend to be based on samples that include a number of uninfor-

mative teeth. The inclusion of these uninformative teeth increases the perceived variation within species and thus swamps out the phyletic signal that might otherwise have been detected. This makes it practically impossible to interpret the fossil record of shark teeth with any degree of reliability, much less trace species lineages through time.

This study presents the results of a comprehensive morphometric survey of tooth-shape variation in extant *Carcharhinus*. Our aim is: (1) to ascertain the extent to which different species can be recognized from their teeth, (2) to determine which teeth are maximally distinctive across species, and (3) to determine a quantitative means by which the maximally distinctive teeth can be distinguished from all other teeth.

It is anticipated that the successful completion of these goals will set the stage for the objective interpretation of phyletic change in *Carcharhinus* tooth shape through the fossil record.



Fig. 2. Upper and lower jaw tooth series from right side of jaw, for typical specimens of the 22 species represented. Upper jaw teeth are represented on the left with their lower-jaw counterparts on the facing page. The fifth upper jaw tooth in each series is shown in silhouette at actual size on the left.

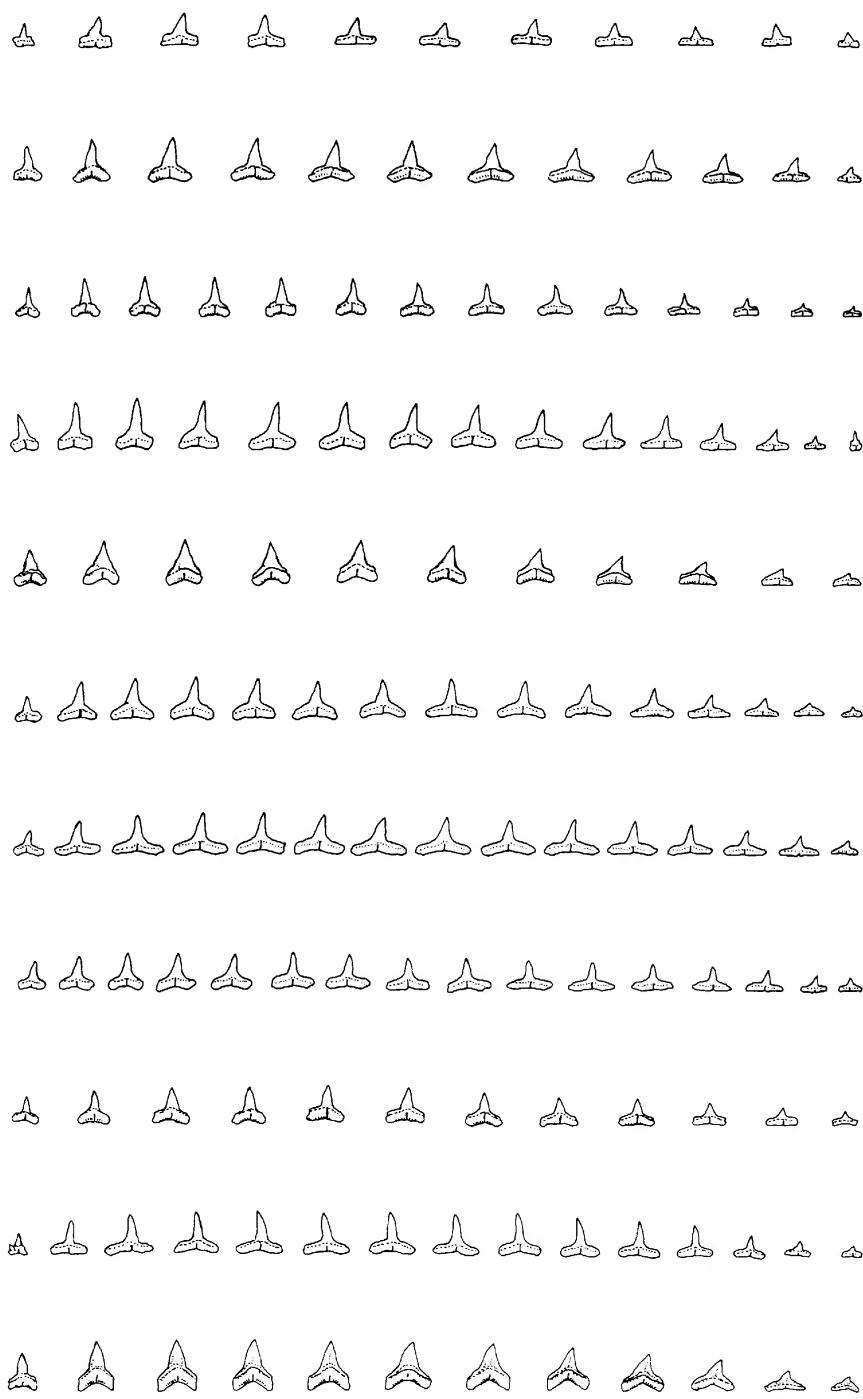


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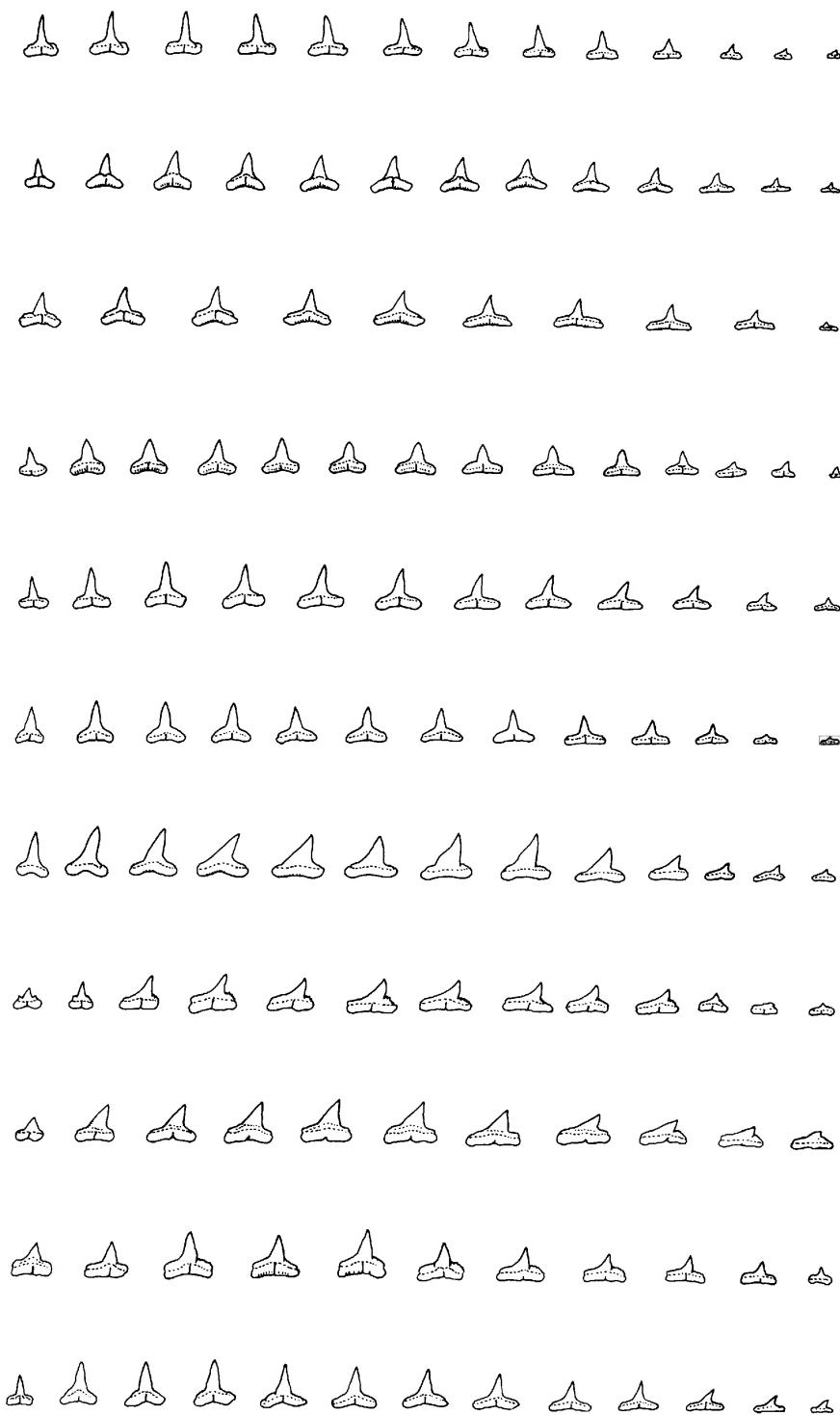


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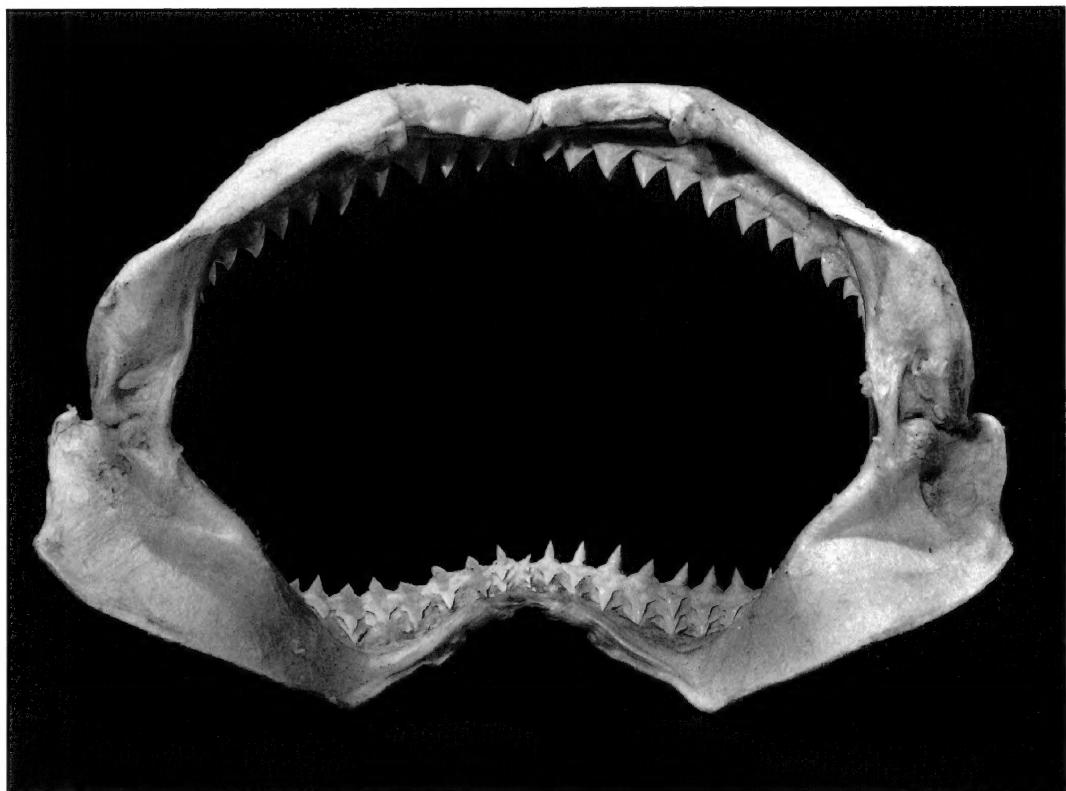


Fig. 3. Bull Shark (*Carcharhinus leucas*) jaw viewed from behind, showing both the erect functional teeth and replacement teeth at sequentially different stages of development.

SOURCES OF VARIATION IN TOOTH SHAPE IN *CARCHARHINUS*

The factors that influence variation in tooth shape in *Carcharhinus* can be divided into three main categories: (1) those due to differences among species, (2) those due to differences among individuals within species, and (3) those due to differences within individuals.

Variation among species is particularly noticeable in the upper jaw teeth (see fig. 2). For the purpose of consistency and clarity we adopt a nomenclature in which teeth in a series are numbered from the central symphysis toward the lateral angle of the jaw. In order to avoid ambiguity, reference is also made to the jaw quadrant from which the tooth originates. Thus the "upper left position 6 tooth" (UL6) refers to the sixth tooth from the central symphysis, on the left-hand side of the upper jaw (see fig. 1).

Within the upper jaw, the teeth between

positions 3 and 8 are generally distinct among species. By contrast, the anterior teeth on either side of the symphysis (positions 1 and 2) and the extreme posterior teeth (positions 10, 11, 12, etc.) seem less distinctive among species. Lower jaw teeth are noticeably less differentiated among species than are the upper jaw teeth.

Variation within species is due to geographic variation, sexual dimorphism, and individual variation. Geographic variation in tooth form does not seem to have any clear environmental correlates, and varies from one species to the next. Some species exhibit slight geographic variation in tooth form, but do not show concordant variation in color pattern, whereas others (*C. limbatus* in particular; Garrick, 1982) show marked geographic variation in color pattern but have similarly shaped teeth throughout their ranges. Sexual dimorphism in tooth shape exists in some species of *Carcharhinus* (Bass et al., 1973; Garrick, 1967; Springer, 1964; Compagno,



Fig. 4. Replacement teeth in a section of the lower jaw in a Bull Shark (*Carcharhinus leucas*). The teeth at the outermost occlusal margin of the jaw are replaced, as if on a conveyor belt, by developing teeth moving out from the inside.

1984). Where seen, it is often more pronounced in anterior teeth, which tend to be narrower and more prominent in males than in females (Springer, 1964; Compagno 1984). Variation among individuals at a given locality does not seem to have clear correlates either. Some species exhibit very little variation among individuals; others exhibit a considerable amount. It is possible that the amount of variation among individuals within a species is tied to the geographic range of the species. Certainly the species showing one of the most restricted ranges in this study, *C. isodon*, shows the least amount of variation among individuals. By contrast, *C. plumbeus*, which has one of the largest ranges of the species surveyed, shows one of the most extensive degrees of tooth-shape variation among individuals within localities. Further investigation is required before conclusions can be drawn, however.

Variation within individuals is the largest source of variation in tooth shape in *Carcharhinus*. We have chosen to investigate four types: (1) **dignathic**—differences in tooth

shape between upper and lower jaws (Applegate, 1965, 1967; Peyer, 1968; Compagno, 1970), (2) **monognathic**—differences in tooth shape associated with tooth position within a tooth series in one quadrant of the jaw (Compagno, 1970), (3) **variation in symmetry**—differences in tooth shape due to side (left or right), and (4) **ontogenetic**—differences in tooth shape associated with the relative maturity of the shark (Peyer, 1968; Compagno, 1970; Reif, 1973). We shall deal briefly with each in turn.

DIGNATHIC VARIATION: The upper jaw teeth of all species within *Carcharhinus*, with the possible exception of *C. isodon*, have a much broader enameloid portion than do their lower jaw counterparts (fig. 2). The upper jaw teeth tend to be used for cutting while the lower jaw teeth are used for grasping. The enameloid portion of teeth in the lower jaw tends to be spikelike and considerably more erect than it is in teeth of the upper jaw.

MONOGNATHIC VARIATION: There is a marked incrementally graded change in size and shape of teeth as one progresses along a

tooth series from the symphysis to the angle of the jaw. This graded change is seen in both upper and lower jaws (fig. 2). Teeth toward the symphysis of the jaw tend to be more erect, while those toward the angle of the jaw are lower crowned and more recurved. Even though different species within *Carcharhinus* have different numbers of teeth per jaw, the same within-jaw trends are seen in tooth series of all species.

VARIATION IN SYMMETRY: Tooth variation in sharks is highly bilaterally symmetrical. Thus teeth on the right side of the jaw symphysis are approximate mirror images of those on the left side in both upper and lower jaws (see fig. 1). However, it should be noted that anomalous individuals have been collected in which teeth are not bilaterally symmetrical in size or shape (Naylor, personal obs.; Maissey, personal commun.).

ONTOGENETIC VARIATION: There appears to be only slight ontogenetic variation in tooth shape within most species of *Carcharhinus*. Most of the variation that does exist seems confined to early juvenile phases where tooth replacement rates are at their highest. Unfortunately, few studies have been carried out to look at ontogenetic variation in teeth of *Carcharhinus*. A notable exception, however, is the study by Raschi et al. (1982), which found very marked changes in tooth form in the ontogeny of *C. signatus*.

Results from the present survey of variation in 12,647 teeth derived from 22 extant members of the genus indicate that within-individual variation in tooth shape—due to: (a) differences between upper and lower jaws, (b) tooth position within a tooth series, and (c) the side of the jaw from which the teeth are taken (left or right)—accounts for 65% of the total tooth-shape variation in the sample. By contrast, the among-species component accounts for only 35% of the total variation in the data set. Small wonder then, that the variation among species, as discrete as it might be for specific comparisons (i.e., Garrick's (1982) upper tooth position "five"), is effectively swamped out by variation within individuals.

Nevertheless, tooth shape varies within individuals in a highly patterned way. As mentioned previously, this pattern is common to all species within the genus (fig. 2). This ob-

servation has allowed us to develop a procedural strategy to filter out a large proportion of the within-individual variation to expose better the 35% variation due to among-species differences. In essence, our procedure partitions within-individual patterns of tooth-shape variation into components that are common to all species. It then makes among-species comparisons in the component determined to be most effective for distinguishing species. The procedure has been designed for use with isolated teeth, where species, age, sex, tooth position, jaw, and side are not known a priori. As such it should be directly applicable to the problem of interpreting the rich fossil record of isolated *Carcharhinus* teeth, assuming that the fossil species exhibit similar patterns of within-individual tooth-shape variation.

METHODS

MATERIAL: 504 dried jaws representing 22 species of *Carcharhinus* were collected from localities throughout the world (See Appendix 1) between 1985 and 1990. Each species was represented, where possible, by samples that included males and females, a range of age classes, and specimens from different geographic localities.

PREPARATION: Teeth were removed from jaws during an eight-week period in July and August of 1989 and a six-week period in September and October of 1990. Teeth were removed from jaws after they had become loosened by soaking in 80°C water for 15 minutes. Upper and lower teeth were then removed and soaked in 4% hydrogen peroxide for 10 minutes to clean off adhering tissue. Teeth were subsequently allowed to dry at room temperature, individually labeled, and placed in a sequential jaw map reflecting their natural positions in the jaw following D'Aubrey (1964). Only teeth from the second series (i.e., the replacement series of teeth immediately behind the erect series at the outermost margin of the jaw), of the right side, were removed and used in this study. Second series teeth were chosen because they are fully formed and in perfect condition. (Teeth from the first, or functional, series tend frequently to be chipped, worn, or broken). Teeth from the left side were not included as they closely

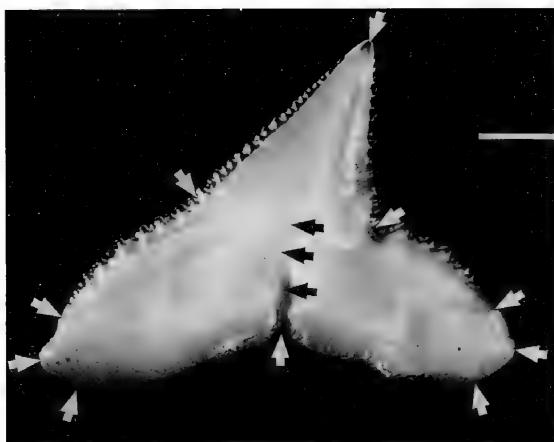


Fig. 5. Fifth upper jaw tooth from *Carcharhinus melanopterus*, the type species for the genus, viewed from the lingual side showing the 13 landmarks recorded. The scale bar represents 1 mm length.

approximate mirror images of their counterparts on the right side. Predicted values for left-side teeth can thus be estimated from the right side data—albeit without variation due to asymmetry. This also allowed us to leave one-half of a set of jaws intact, as a voucher for subsequent reference and comparison.

MEASUREMENT: Teeth were measured using a video digitizing system comprising a Cohu model 4815 chip camera, a PC VisionPlus frame grabber board, a high-resolution Panasonic WV-5490 black-and-white monitor, an EPSON Equity III+ (AT compatible) computer, an adjustable camera stand and the digitizing software package CODA (Haake, 1988). Teeth were placed labial side down on a stage under the camera. The stage was housed in a light diffuser box designed by Dr. Walton Barton Elvers to illuminate specimens optimally. Images of each tooth were viewed on the high-resolution black-and-white monitor. Each tooth was magnified to fill the screen. One consequence of this magnification procedure is that smaller teeth tended to be measured at larger magnifications, causing measurement errors on small teeth to be proportionally smaller than those taken on large teeth. (This is noteworthy only because the opposite situation obtains when measurements are made with hand-held calipers.) At the appropriate magnification and focus, the scale and specimen identification were recorded. The positions of 13 “land-

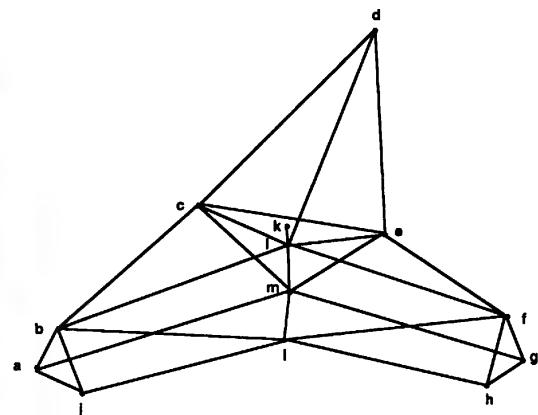


Fig. 6. The 27 linear measurements computed from the 13 landmarks (a–m) depicted in figure 5.

mark” points, A–M (fig. 5) were sequentially located and recorded as X,Y cartesian coordinates in assigned computer files.

Twenty-seven homologous linear distances were computed from the X,Y coordinates for each tooth (fig. 6). These distances were chosen a priori to capture aspects of tooth-shape variation in the data set. It is noteworthy that the curved profiles on both the symphysial and the lateral edges of teeth, which are often quite distinctive for certain species (Garrick, 1982), were poorly captured by these techniques. Similarly, the variation in serration patterns, also distinctive for many species, was not captured.

The 27 distances were stored as variables in a file together with the corresponding values for the variables *species*, *id* (the individual from which the tooth was extracted), *jaw* (upper or lower), *tooth position* in a series (numbered sequentially from the symphysis to the lateral angle of the jaw), *sex*, *maturity*, *total length* of the shark, and *centroid size* of the tooth (computed as the sum of the squared distances from all of the outline X,Y coordinates to the centroid of the tooth [Bookstein, 1991]). The categorical values for maturity (juvenile, subadult, and adult) were assigned based on total length. Teeth from sharks with total lengths less than halfway between the mean length at birth for the species and the mean length at maturation (taken from Compagno, 1984) were assigned to the juvenile category. Teeth from sharks with total lengths above the mean length at matu-

ration for the species, were assigned to the adult category. Teeth were assigned to the subadult category if they fell between the juvenile and adult category. Teeth for which total length data were unavailable were not assigned a value for maturity.

These data (12,647 observations and 35 variables) were loaded onto the City University of New York IBM 370 VM ESA mainframe computer where they were manipulated and subjected to a series of multivariate statistical analyses using the statistics package SAS version 6.05.

PRELIMINARY DATA MANIPULATION AND ASSUMPTIONS FOR ANALYSIS

MIRROR IMAGING: When the teeth from the right side of both upper and lower jaws from any one specimen are laid labial surface down, in the same orientation (enameloid portion pointing toward the top of the page and the root portion toward the bottom of the page), teeth from the upper jaw can readily be distinguished from those of the lower jaw because they tend to be "angled" in different directions—"uppers" to the right, "lowers" to the left. Confusion between upper and lower teeth thus rarely arises when comparing teeth from one side of the jaw. However, if upper and lower teeth from both sides of the jaw are contrasted simultaneously, then teeth from the lower right tend to be "angled" in the same way as are teeth from the upper left, and vice-versa (see fig. 7), potentially confounding the correct assignment of teeth to their corresponding jaw (upper or lower).

In this study teeth were extracted only from the right side of both the upper and lower jaws for each specimen. The left side of all jaws was left intact. Voucher specimens (jaws with teeth from the right side, second series, removed) for those samples collected expressly for this survey have been deposited at the Department of Ichthyology at the American Museum of Natural History. Specimens loaned from other institutional collections (e.g., the J. L. B. Smith Institute of Ichthyology) are annotated in Appendix 1.

Tooth form in sharks shows a high degree of bilateral symmetry. This has allowed us to estimate data for the left side by translating right side data to its mirror-image equivalent.

It should be noted that this procedure necessarily excludes any differences due to bilateral asymmetry that might exist between the two sides of the jaw. For the purposes of this study, such differences are assumed to be negligible.

TRANSFORMATION: Analyses using log-transformed data were initially carried out on the entire data matrix but were not found to add substantial interpretability. As a result, all statistical analyses were made using raw distances (recorded in millimeters).

INDEPENDENCE: All of the multivariate statistical analyses carried out on the data set have optimal properties if the assumption of independence obtains—that is, if the observations from different individual teeth are independent of one another. This assumption is violated throughout the study because representative teeth from different positions in both jaws of the same individual are included in the data set (approximately 25 teeth per shark). However, because teeth vary markedly in shape at different tooth positions in a series, and in different jaws of the same individual, the assumption of independence is not violated in a way that corresponds directly to simple replication of observations. Instead, it corresponds to a form of pseudo-replication, the exact influence of which is unknown. However, it undoubtedly inflates the degrees of freedom and F statistics in the analyses. In view of these inherent pseudo-replication problems, we have relied less on the computation of confidence intervals, test statistics, and the p values based on them, and have instead concentrated on verifying initial predictions, based on random splitting of the data set. Predictions based on one portion of the data set were tested with "unseen" observations from the other. Thus, for example, when attempting to discriminate teeth by species we partitioned the entire data set into a calibration or "training" data set and a "test" data set (SAS, 1988). We computed discriminant functions using the "training" data set and then tested their discriminatory power using the "test" data set. In this way, we were able to test our procedures rigorously while circumventing some of the shortcomings caused by the violation of the assumption of independence.

HOMOGENEITY OF COVARIANCE: Many of

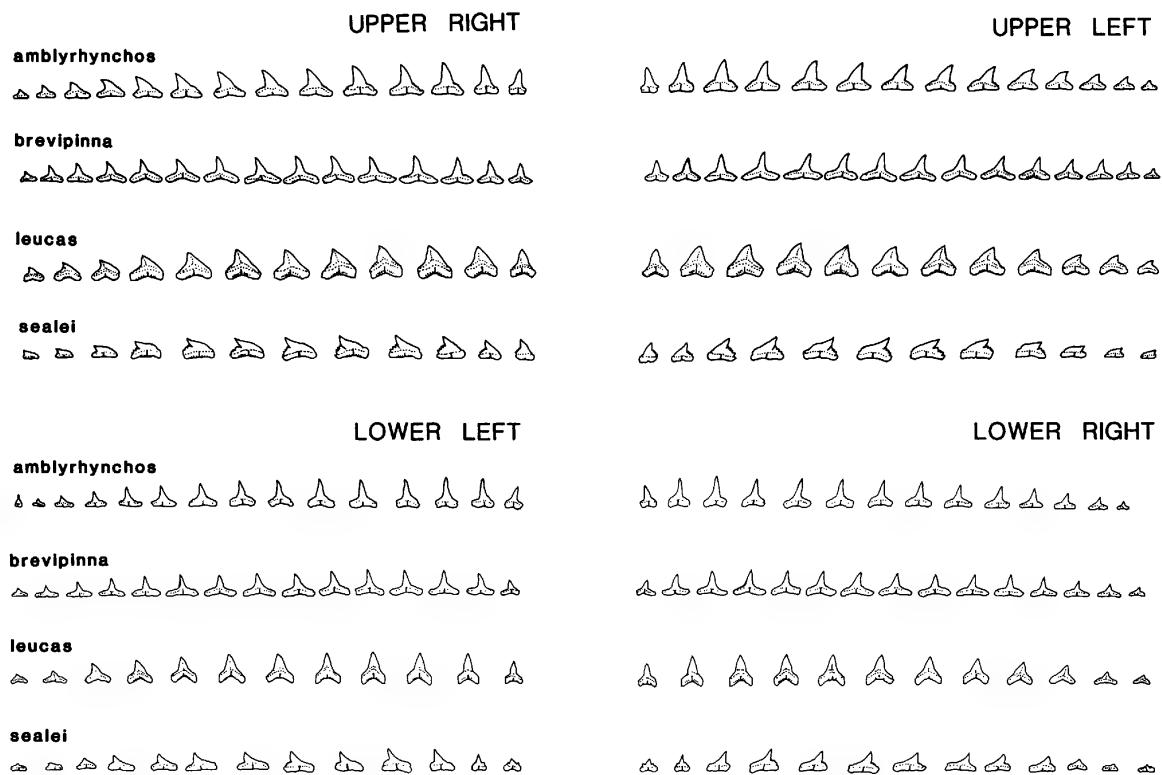


Fig. 7. Teeth from four species, *C. amblyrhynchos*, *C. brevipinna*, *C. leucas*, and *C. sealei*, depicting upper and lower jaw, left and right side teeth adjusted for size differences between species to facilitate comparison. Shown in same orientation on page (tooth base toward bottom of page, tooth crown toward top). Note that teeth from the upper left quadrant of the jaw are angled in the same way as are those from the lower right, and that teeth from the upper right are angled in the same way as are the teeth from the lower left. This similarity contributes to uncertainty in tooth position assignment in opposite quadrants of the jaw.

the classical multivariate analyses have optimal properties when the data for each of the groups under investigation have homogeneous covariances. That is, the analyses are most efficient when the different groups being compared have similar dispersion characteristics. Linear discriminant analysis and canonical variate analysis, for example, require the pooled within-group covariance of all the groups. The extent to which different groups have different covariances (different dispersion characteristics) influences the validity of the procedures. If each of the groups comprises a cluster of the same size, shape and orientation, then the analysis will be optimal. If clusters, corresponding to different groups have different inflations and/or different orientations, then the procedure will produce

more incorrectly assigned observations, all else being equal.

There are multivariate analyses designed for use with data sets in which groups are known to have heterogeneous covariances, (i.e., data sets in which the dispersion characteristics are known to be different among groups). One such procedure is quadratic discriminant analysis, in which the within-group covariances are not pooled, but are considered separately for each group. When covariances are not homogeneous, the quadratic discriminant analysis is theoretically better in terms of assigning observations correctly, than is a linear discriminant analysis. However, because the covariances are not pooled across groups, the sample sizes required to establish reliable quadratic discriminant

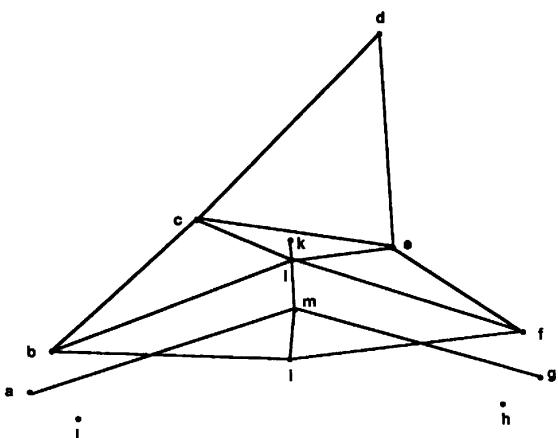


Fig. 8. The 16 linear measurements determined to be optimal for species discrimination by a combination of subjective assessment, Krzanowski cross-validational principal component analysis, and stepwise discriminant analysis.

functions (for use with "unseen" test data sets) are generally much larger than they are for linear discriminators. As a result, when sample sizes are small, one can sometimes correctly assign more observations in an unseen "test" data set, using a linear discriminant analysis, than one can using a quadratic discriminant analysis based on the same "training" data set, even though the within-group covariances are significantly different from one another.

In this survey, tests for homogeneity of covariances (Bartlett's modification of the likelihood ratio test [Morrison, 1976]) generally indicated that the covariance structure among groups is significantly different. Nonetheless, we found that linear discriminant analysis resulted in more correct assignments to species, when applied to the "test" data set, than did the quadratic discriminant analysis. We conclude that larger sample sizes are needed to reap the advantages inherent in quadratic discrimination. (Note that sample sizes used for discrimination by tooth position were large enough to make effective use of quadratic discriminant analysis.)

SAMPLE SIZES AND NUMBER OF VARIABLES USED IN ANALYSIS: Sample sizes required to attain statistical confidence are strongly influenced by "how many different effects one tries to address with the data" and "how many

measurements are used to address them." Generally, strong and clear effects can be summarized with fewer (appropriately chosen) measurements than are necessary for weak and confounded effects.

In this study a number of different analyses were carried out, each with different sample size constraints. For example, the linear discriminant analysis by species could only be applied to a subset of the original data, because we were obliged to set the sample size per species to a level commensurate with the sample size of the most poorly represented species in the survey. This was done to avoid biasing the pooled-within covariance toward those species that were best represented in the original sample.

Although 27 measurement variables (traits) were initially recorded for each tooth, satisfactory results were frequently achieved with a subset of these variables. This is due primarily to the fact that many of the variables are highly correlated and are thus implicitly "predicted" by combinations of other variables, and secondarily because some variables were simply not informative. We have endeavored to use the smallest number of variables to achieve satisfactory results, both to simplify interpretation and to improve statistical power.

Subsets of variables were selected using three independent methods: (1) subjective assessment—variables were preferentially included in the subset if they were thought to convey information about tooth-shape variation among species; (2) stepwise discriminant analysis; (3) cross-validational principal component analysis (Krzanowski, 1987; Reymert, 1991). This procedure, while originally designed for principal component cross-validation, has been found to be effective for selecting subsets of variables useful for discriminant analysis (Stuenes and Marcus, 1991). There was considerable concordance among all three methods, but most strikingly between the subjective assessment and the Krzanowski synthesis. The final selection of variables included all 12 of the variables suggested by the Krzanowski procedures and 4 more suggested by both subjective assessment and the stepwise discriminant procedures. The final choice of variables is presented in figure 8.

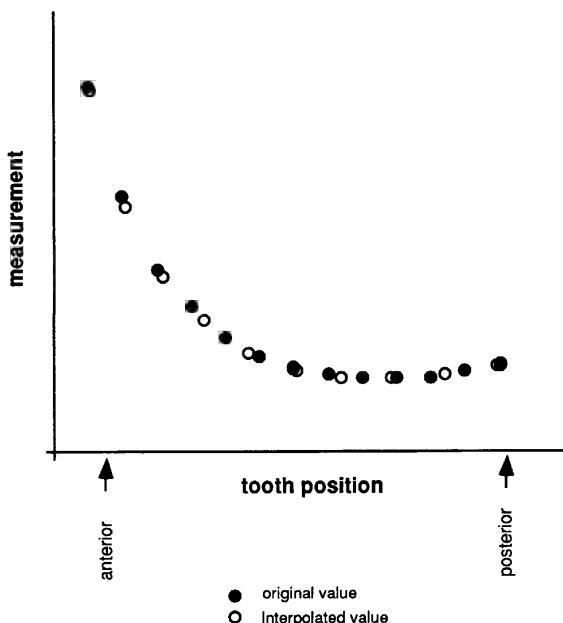


Fig. 9. Different species of *Carcharhinus* have different numbers of tooth positions per tooth series, making homologous comparisons by tooth position problematic. To circumvent this problem we created a pseudotooth series for each individual shark represented in the data set. Each pseudotooth series contains 10 teeth regardless of the number of teeth in the original tooth series. This enables comparisons to be made across "pseudohomologous" tooth positions. The positionally homologous pseudoteeth were created by interpolation of original tooth measurements. Thus a specimen originally containing 13 teeth in a series would yield 10 pseudoteeth derived from these 13. Each of the pseudoteeth would contain 1.3 or 13/10 "original tooth positions worth" of data (see text for more detailed explanation and table 1 for specific examples). The homologizing procedure is represented graphically for one variable. Measurements are taken for each of 13 teeth in a tooth series, and are plotted against their corresponding tooth positions in the tooth series (filled circles). The 10 measurements (interpolated from the original 13), used as pseudotooth data, are shown overlain (open circles) on the original measurements. Notice that the original form of the trajectory representing measurement variation across a tooth series is maintained in the pseudotooth data set even though fewer points are used to represent the trajectory.

TOOTH POSITION HOMOLOGY: Different species of *Carcharhinus* vary in the numbers of tooth positions they typically have in a tooth series. *C. acronotus*, for example, typically has 12 teeth on either side of the symphysis in the upper jaw. *C. brevipinna*, by contrast, typically has 16 (see fig. 2). This variation among species exists for both upper and lower jaws. There is also variation in the number of teeth contained in a tooth series *within* species. The range of variation within species is generally much smaller than that seen among species (rarely exceeding a difference of one tooth position per tooth series [Garrick, 1982]).

The variation in the number of tooth positions per tooth series poses a problem if

teeth are to be homologized by their position across different species. If teeth are "homologously aligned" one at a time, starting at the symphysis and working toward the angle of the jaw (in such a way that position 1 in species A corresponds to position 1 in species B, position 2 in species A corresponded to position 2 in species B . . . etc.), then species that generally had higher numbers of teeth (e.g., *C. brevipinna*) would have "floating" posterior teeth with no assignable homologs in other species. The converse is, of course, true if teeth are homologized in the reverse direction, from the angle of the jaw toward the symphysis (La Duke, 1991).

We have adopted a system for aligning tooth position across species that is based on

TABLE 1
Compositional Breakdown of Pseudotooth Measurements

(The fraction of each original tooth measurement used for the computation of pseudotooth measurements. Numbers in parentheses correspond to original tooth position number. See text for details.)

No. of teeth	Pseudotooth positions (A-E)				
	A	B	C	D	E
11	(1)+.1(2)	.9(2)+.2(3)	.8(3)+.3(4)	.7(4)+.4(5)	.6(5)+.5(6)
12	(1)+.2(2)	.8(2)+.4(3)	.6(3)+.6(4)	.4(4)+.8(5)	.2(5)+.6(6)
13	(1)+.3(2)	.7(2)+.6(3)	.4(3)+.9(4)	.1(4)+(5)+.2(6)	.8(6)+.5(7)
14	(1)+.4(2)	.6(2)+.8(3)	.2(3)+(4)+.2(5)	.8(5)+.6(6)	.4(6)+.7(7)
15	(1)+.5(2)	.5(2)+(3)	(4)+.5(5)	.5(5)+(6)	(7)+.5(8)
16	(1)+.6(2)	.4(2)+(3)+.2(4)	.8(4)+.8(5)	.2(5)+(6)+.4(7)	.6(7)+.8(8)
No. of teeth	Pseudotooth positions (F-J)				
	F	G	H	I	J
11	.5(6)+.6(7)	.4(7)+.7(8)	.3(8)+.8(9)	.2(9)+.9(10)	.1(10)+(10)
12	(7)+.2(8)	.8(8)+.4(9)	.6(9)+.6(10)	.4(10)+.8(11)	.2(11)+(12)
13	.5(7)+.8(8)	.2(8)+(9)+.1(10)	.9(10)+.4(11)	.6(11)+.7(12)	.3(12)+(13)
14	(8)+.4(9)	.6(9)+.8(10)	.2(10)+(11)+.2(12)	.8(12)+.6(13)	.4(13)+(14)
15	.5(8)+.9(9)	(10)+.5(11)	.5(11)+(12)	(13)+.5(14)	.5(14)+(15)
16	(9)+.6(10)	.4(10)+(11)+.2(12)	.8(12)+.8(13)	.2(13)+(14)+.4(15)	.6(15)+(16)

the assumption that the dental lamina, from which all teeth develop in these sharks, is homologous across species. We assume that there is a tooth position gradient running from the symphysis to the angle of the jaw as seen in figure 2. We assume that tooth positions at the symphysis (extreme anterior) of the jaw and that tooth positions at the angle (extreme posterior) of the jaw are homologous across species. We assume that the region in between is divided into a different number of equally sized subunits in the different species. Thus in *C. brevipinna* the dental lamina is divided into 16 "tooth-position subunits" while in *C. acronotus*, it is divided into 12.

We have implemented a protocol, based on these assumptions, that creates a new "homologously aligned" pseudotooth data set of measurements in which all individual sharks are seen to have only 10 teeth per series, regardless of their original tooth count. The "homologously aligned" pseudotooth data set is represented by 10 teeth (rather than any other number, which could serve equally well), as this represents the smallest number of tooth positions that occur in any of the tooth series examined by us (seen in *C. acronotus* and *N. velox*).

The "homologizing" protocol interpolates measurements between the original tooth positions for each tooth series in the data set. For example, if measurements that correspond to 10 homologously aligned pseudoteeth are to be extracted from a tooth series containing 13 original teeth, each pseudoteeth in the "homologously aligned" pseudotooth data set must contain information from 1.3 (13/10) original teeth. The first pseudotooth thus comprises all of the information from the first original tooth added to 30% of the information from the second original tooth, to total 130% "original tooth positions worth" of information. The second pseudotooth will comprise 70% of the information from the second original tooth (i.e. the amount of the second original tooth information "left over" from the first pseudotooth calculation) added to 60% of the information from the third original tooth, to total 130% "original tooth positions worth" of information, once again. The third pseudotooth will comprise 40% of the information from the third original tooth (i.e., the amount of the third original tooth information "left over" from the second pseudotooth calculation) added to 90% of the information

from the fourth original tooth, to total 130% "original tooth positions worth" of information, and so on. (Note that if a tooth series contained 16 original tooth positions, as would be the case for *C. brevipinna*, then each of the resultant ten pseudoteeth would contain 160% (16/10) "original tooth positions worth of information." Refer to table 1 for examples of each different case. The procedure was carried out separately for each of the 504 pairs of tooth series (upper and lower) and for each of the 27 linear measurement variables in the data set. (Note that there are 504 individuals represented in the data set, each represented by an average of 24 teeth, and each tooth being measured for 27 linear distance variables.)

The effect of this "homologizing realignment procedure" is perhaps most readily appreciated graphically (fig. 9). If the original values of a selected variable are plotted against their corresponding tooth positions for each tooth in a series, then the curve fitted through these points represents the tooth series trajectory for the variable under scrutiny, for the jaw in question. The "homologizing protocol" effectively determines new values for the variable under scrutiny at 10 equally spaced intervals along the trajectory.

It is possible that this method of aligning teeth in different species forces nonhomologous comparisons to be made. For example, it is possible that the first four tooth positions in *C. brevipinna* are homologous to the first tooth position in *C. acronotus*. However, given that all teeth seem to have fairly similar shape trajectories over tooth positions (see fig. 2), we feel that our method provides a reasonable and parsimonious first approximation to a concept of positional homology, though we freely admit that alternative explicit hypotheses have not been tested. Empirical results from discriminant analyses suggest that the alignment procedure does not interfere with the species-specific tooth-shape signal in the data.

For the sake of clarity, pseudoteeth in the "homologized" data set will be referred to using alphabetic tooth position notation, to contrast with teeth from the original data set. Thus the "upper left position F tooth" (ULF) refers to the sixth tooth along from the central

symphysis of the left upper jaw in the homologized pseudotooth data set, whereas UL6 refers to the sixth tooth along from the central symphysis of the left upper jaw in the original tooth data set.

SIZE: Size differences among species facilitate discrimination among species. Ontogenetic size differences within species confound size-based discrimination among species. If we are to benefit from size-based differences among species, and avoid the confusion brought about by the ontogenetic size differences within species, we must first be able to determine a priori whether a tooth came from an adult or a juvenile shark. This is not possible for the isolated teeth in the fossil record, as one cannot readily distinguish the juvenile teeth of some large species from the adult teeth of some smaller species.

Because of this difficulty, and because our central aim is to provide a framework to interpret the fossil record of shark teeth, we have elected to ignore information concerning the size of teeth and have adjusted for size. All analyses reported in this survey are therefore carried out "size-free." That is, all teeth have been standardized to the same size. This has been achieved by dividing all measurements through by the square root of centroid size of the corresponding tooth. (Centroid size is computed as the sum of the squared distances from all of the outline X, Y coordinates to the centroid of the tooth; Bookstein, 1991.)

MISSING DATA: A number of teeth in the original sample were chipped or worn in such a way that it was not possible to record the full complement of landmarks for the observation. In such cases it was not possible to compute all 27 distances.

The procedure employed for homologizing tooth position described above is strongly affected by missing data. The interpolation method used is based on simultaneous weighted averaging of values derived from two or three teeth at a time (see table 1). Single teeth in the original data set thus influence the values of variables assigned to two or three adjacent pseudoteeth in the homologized data set. If an original tooth has missing data, the pseudoteeth that partially derive from it will be entered as missing data. A

missing value in one original tooth can thus result in two or three pseudoteeth having missing values. In short, the process used to "homologize" tooth position in the jaw magnifies the gaps in the data.

In order to minimize this effect, we adopted a procedure to fill in as much of the missing data as possible prior to creating the homologized pseudotooth data set. We estimated values for those teeth in the original data set that were missing data, but that were flanked on both sides by teeth from which reliable measurements could be taken. The procedure was carried out one variable at a time, for all 27 distance variables in the data set. Each tooth with missing data was assigned the average of the value of its two flanking teeth, for the variable under scrutiny. By "filling in" values for the teeth with missing data in this way, we were able to minimize the loss of data which would otherwise have been brought about by the subsequent procedure for homologizing tooth position. We consider this a reasonable procedure given the smooth and incrementally graded change in tooth shape along a tooth series.

It is possible that the statistical analyses carried out on the homologized pseudotooth data set may have been influenced by the combined effects of the two interpolations used ("filling in" and creating the pseudotooth data set). However, it should be noted that the predictions that were based on the pseudotooth data set were all verified with tests carried out on the original data set, which did not include missing data.

ANALYSIS: A large number of analyses were carried out on this data set. We have grouped them into three parts that correspond to the three questions listed below.

1. Are some teeth better than others for distinguishing among species? Garrick (1982) pointed out that the upper jaw teeth were more variable among species than the lower teeth. He chose the fifth tooth from the symphysis in the upper jaw as the exemplar for each species (Garrick, 1982: 15). It is likely that this tooth position (position 5 in the upper jaw) is one of the better ones for discriminating among species.

We performed a linear discriminant analysis by species for a data set containing the 16 tooth measurements selected to best discriminate among species (fig. 8). Each of the 22 species was represented by tooth series from eight randomly chosen individuals (with the exception of *C. wheeleri* for which only five individuals were available and *C. sorrah* for which only six individuals were available). The analysis was carried out using the data set comprising the original tooth measurements, but was restricted to teeth from the right side of the jaw. Separate analyses were carried out for the upper and the lower teeth. Results were validated using the "cross-validation" option available in SAS 6.05. This option removes observations, (individual teeth in this case) one at a time, and recomputes the discriminant analysis. Observations that were incorrectly assigned by the discriminant procedure were sorted by their tooth position in the series. A plot of the incorrectly assigned observations sorted by tooth position and expressed as a percentage is presented for the upper teeth in plot A, and for the lower teeth in plot B, of figure 10. Three things should be noted: (1) The upper jaw teeth are assigned to species correctly more often than are the lower jaw teeth; (2) both the extreme anterior (tooth positions 1 and 2) and the extreme posterior teeth (tooth positions 11–16) are more frequently misassigned to species than are the more centrally placed teeth; and (3) most of the centrally placed teeth (positions 3 to 10) are misassigned to species with approximately the same frequency.

The finding that most of the centrally placed teeth are misassigned with the same frequency reflects the fact that the most distinctive teeth, i.e., those optimal for discrimination among species, are found at slightly different tooth positions in different species. This is consistent with the observation that different species vary in the number of tooth positions they have per series (for example, the optimal tooth position in *C. acronotus*, which typically has 12 teeth per series might be position 6, whereas the optimal tooth position in *C. brevipinna* which typically has 16 teeth per series might be position 8).

In an effort to minimize the hypothesized variation in optimal tooth position across

species, a linear discriminant analysis was carried out using the "homologously aligned pseudotooth data set," containing 10 teeth per tooth series. Once again, the analysis was restricted to teeth from the right side of the jaw and was carried out separately for the upper and lower teeth. The plot of the incorrectly assigned observations, sorted by tooth position and expressed as a percentage, is presented for the upper teeth in plot C and for lower teeth in plot D of figure 10.

Results from the pseudotooth data reflect the same general pattern seen for the original tooth data, namely that the upper teeth are assigned to species correctly more often than are lower teeth and that both the extreme anterior and the extreme posterior teeth are assigned to species correctly less often than are the more centrally placed teeth. However, results differ significantly in that among the centrally placed teeth of the upper jaw (pseudopositions C–H), two tooth positions (E and F) stand out as being better than any others for among-species discrimination. This lends support to the idea that the "homologizing realignment procedure," used to create the pseudotooth data, has resulted in the convergence of disparate optimal tooth positions among different species in the original data to a more focused region of the jaw in the pseudotooth data set. An alternative plausible interpretation is that the apparent convergence is nothing more than a smoothing artifact brought about by the interpolation used to create the pseudotooth data set.

The result that overall discrimination appears to be better for the pseudotooth data than it is for the original tooth data is somewhat disquieting. In the original data 44.8% of the teeth were incorrectly assigned to species, whereas the result for the pseudotooth data set was 38.18%. One would not predict that the process of creating the pseudotooth data set should bring about any change in the effectiveness of discrimination. It is possible that some of this change is caused by the smoothing procedures involved in "filling in" missing data and in "homologizing" tooth position. However, it is more likely that the disparity is a consequence of differences in sample size heterogeneity between the two analyses. To elaborate, linear discriminant analysis performs most effectively when there

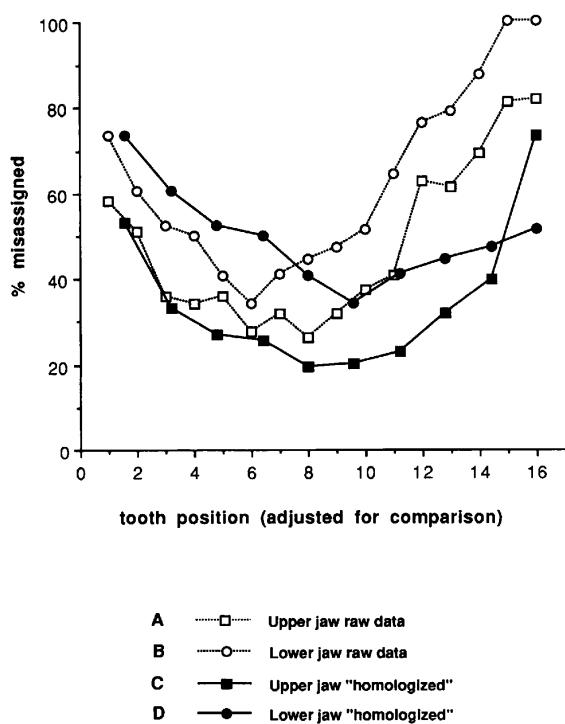


Fig. 10. Teeth misassigned to species arranged by tooth position within a tooth series. Tooth position categories have been adjusted to facilitate direct comparison between the four plots A, B, C, and D.

is homogeneity in the covariance matrices and when sample sizes do not differ too greatly. (This condition is more likely to be satisfied when the sample sizes of the various classes to be discriminated are the same.) For the original data, each species was represented by eight randomly chosen individuals. Thus, *C. brevipinna* was represented by 128 teeth (8 individuals \times 16 teeth per jaw), *C. acronotus* was represented by 96 teeth (8 individuals \times 12 teeth per jaw) etc. With the homologously aligned pseudotooth data, all species were represented by eight randomly chosen individuals, each of which contained exactly 10 teeth, regardless of species. The design using the pseudotooth data set was thus more "balanced", having exactly 80 teeth per species (*C. wheeleri* and *C. sorrah* excepted), than was the design using the original data, where sample sizes ranged from 96 to 128 observations per species. It is likely that this difference in "balance" between the two

	acronotus	albimarginatus	altimus	amblyrhynchos	amboinensis	brachyurus	brevipinna	falciformis	galapagensis	isodon	leucas	limbatus	longimanus	melanopterus	obscurus	perezi	plumbeus	porosus	sealei	sorrah	velox	wheeleri	
acronotus	14 87.5					1																1	
albimarginatus		15 93.75																				1	
altimus			15 100																				
amblyrhynchos				14 87.5																		1	
amboinensis					16 100																		
brachyurus						16 100																	
brevipinna							16 100																
falciformis								14 87.5															
galapagensis	1		2					12 75															
isodon									16 100														
leucas			1					1		14 87.5													
limbatus											15 100												
longimanus									4	1	10 82.5			1									
melanopterus												16 100											
obscurus								1					14 87.5			1							
perezi													1		15 93.75								
plumbeus		1													15 93.75								
porosus																16 100							
sealei																	16 100						
sorrah																		12 100					
velox		1					1												14 87.5				
wheeleri		1	1																	8 80			

Fig. 11a. Classification matrix resulting from a linear discriminant analysis by species based on 16 tooth measurements taken from pseudoteeth E and F in eight randomly selected individuals for each of the 22 species represented in the study. (Note that *C. wheeleri* and *C. sorrah* were represented by five and six individuals, respectively, in the data set.) Rows correspond to true species identities, columns to assignment categories. Correctly assigned observations thus fall into the diagonal cells of the array. The number of observations assigned to different cells of the matrix are depicted in bold type. Correctly assigned values are also expressed as percentages (small type) in diagonal cells. The matrix reflects the classification accuracy for the reassignment of teeth to their correct species categories. Notice that the observations that were used to determine the discriminant functions were themselves reassigned. (Assignment accuracy is thus likely inflated as the same observations are being used, both to create, and to test the classification model.) The discriminant functions derived from this calibration data set were retained for subsequent use with a "test" data set (see fig. 11c).

analyses accounts for some of the improved performance in the discriminant analysis of the pseudotooth data set.

The above findings are loosely consistent

with Garrick's (1982) choice of the fifth upper tooth as an appropriate exemplar tooth to represent species differences. Be aware, however, that Garrick chose the fifth upper tooth

	acronotus	albimarginatus	altimus	amblyrhynchos	amboinensis	brachyurus	brevipinna	falciformis	galapagensis	isodon	leucas	limbatus	longimanus	melanopterus	obscurus	perezi	plumbeus	porosus	sealei	sorrah	velox	wheeleri
acronotus	13 81.25				1							1										1
albimarginatus		13 81.25														1					1	1
altimus			15 100																			
amblyrhynchos				12 75											1							3
amboinensis					15 93.75							1										
brachyurus						15 93.75					1											
brevipinna							16 100															
falciformis								13 81.25									1	1	1			
galapagensis	1	1	2						11 68.75							1						
isodon										16 100												
leucas				1					1		14 87.5											
limbatus					2							13 86.67										
longimanus							4		1	10 62.5			1									
melanopterus											16 100											
obscurus	1	2			1								10 62.5			2						
perezi												1		14 87.5							1	
plumbeus	1	1											2		12 75							
porosus															16 100							
sealei						1											15 93.75					
sorrah																	12 100					
velox	1				1													14 87.5				
wheeleri		1	3												1					5 50		

Fig. 11b. Results from the discriminant analysis depicted in figure 11a after cross-validation, which computes a series of discriminant analyses excluding a different observation from the data set in each run. The excluded observations are reassigned during the course of each run using the posterior probabilities derived from the rest of the observations in the data set. The classification accuracy for the cross-validated analysis is thus almost always less than that seen for the original calibration analysis depicted in figure 11a.

regardless of the variation in tooth position number across species. Tooth positions E and F of the pseudotooth data (which are the positions selected by the discriminant analysis as being optimal for species discrimination) suggest different original tooth positions for different species. For instance, they represent positions 6 and 7 for *C. acronotus*, but positions 8 and 9 for *C. brevipinna*.

In both of the above analyses, species were represented by eight randomly chosen individuals. Each of the individuals was represented by multiple teeth from different tooth positions, within the same tooth series. The inclusion of these nonindependent multiple observations from the same individuals may bias the discriminant analysis to suggest better discrimination than is actually possible

	acronotus	albimarginatus	altimus	amblyrhynchos	amboinensis	brachyurus	brevipinna	falciformis	galapagensis	isodon	leucas	limbatus	longimanus	melanopterus	obscurus	perezi	plumbeus	porosus	sealei	sorrah	velox	wheeleri
acronotus	33 91.67									1										1	1	
albimarginatus																						
altimus		29 96.67								1												
amblyrhynchos					20 83.33																	
amboinensis						37 84.00	1			1				4								
brachyurus		1					34 91.89	1									1	2				1
brevipinna													2									
falciformis	1		2					48 71.84	2				1		1	4	4	3				1
galapagensis		3	1	1					20 66.67			1		4								
isodon										24 100												
leucas			9						2		44 73.33		5									
limbatus			1		2				8		61 82.43						2					
longimanus									3			28 87.5		1								
melanopterus																						
obscurus	1		4					2	1	4				17 54.84		2						
perezi														5 83.33	1							
plumbeus								2						1	1	35 87.5						
porosus			7											3	3	13 46.43	1	1				
sealei	2																15 83.33	1				
sorrah																						
velox																					22 100	
wheeleri																						

Fig. 11c. Classification matrix by species for a "test" data set. The "left over" observations in the data set that were *not* used in the original computation of linear discriminant functions were subjected to a posteriori assignment. The classification accuracy depicted is a realistic reflection of the accuracy with which unseen observations might be classified. Notice that there are no entries in the matrix for teeth from *C. albimarginatus*, *C. amblyrhynchos*, *C. melanopterus*, *C. wheeleri*, and *C. sorrah*. These are species that were represented in the original data set by eight or fewer individual sharks per species. They were thus used in the creation of the calibration or "training" data set but were not sufficiently numerous to be represented in the "test" data set.

(see section on pseudoreplication above). However, it is important to note that these analyses were carried out to investigate the *relative* performance of different tooth positions for discrimination among species, not to see how well species could be distinguished, and so as such, are valid.

In order to determine how well species could be distinguished, we performed a linear discrimination by species using tooth positions E and F from the upper right jaw of the homologously aligned pseudotooth data set. Positions E and F were chosen because they had been previously determined to be opti-

mal for among-species discrimination. The same 16 preselected tooth measurement variables, used to assess the relative performance of different tooth positions for among-species discrimination (fig. 8) were used in the analysis. The data were divided into a "training" set and a "test" set. The "training" set, used to construct the discriminant functions, contained eight randomly chosen individuals per species, each one represented by two teeth, one from position E and one from position F. (Note again, that *C. wheeleri* and *C. sorrah* were represented by five and six individuals, respectively.) The "test" data set, used to test the effectiveness of the discriminant functions computed by the "training" data set, comprised all those teeth from positions E and F that were not used in the "training" data set.

Three tests were carried out on the data set. The first (a) consisted of a discriminant analysis of the "training" data set, where the observations used to create the discriminant functions were themselves reassigned using posterior probabilities. The second (b) consisted of a discriminant analysis of the "training" data set with cross-validation. The third (c) consisted of a discriminant analysis of the "training" data set, tested against the observations in the "test" data. This third test is the most rigorous because it is, in effect, a blind test of the discriminant function.

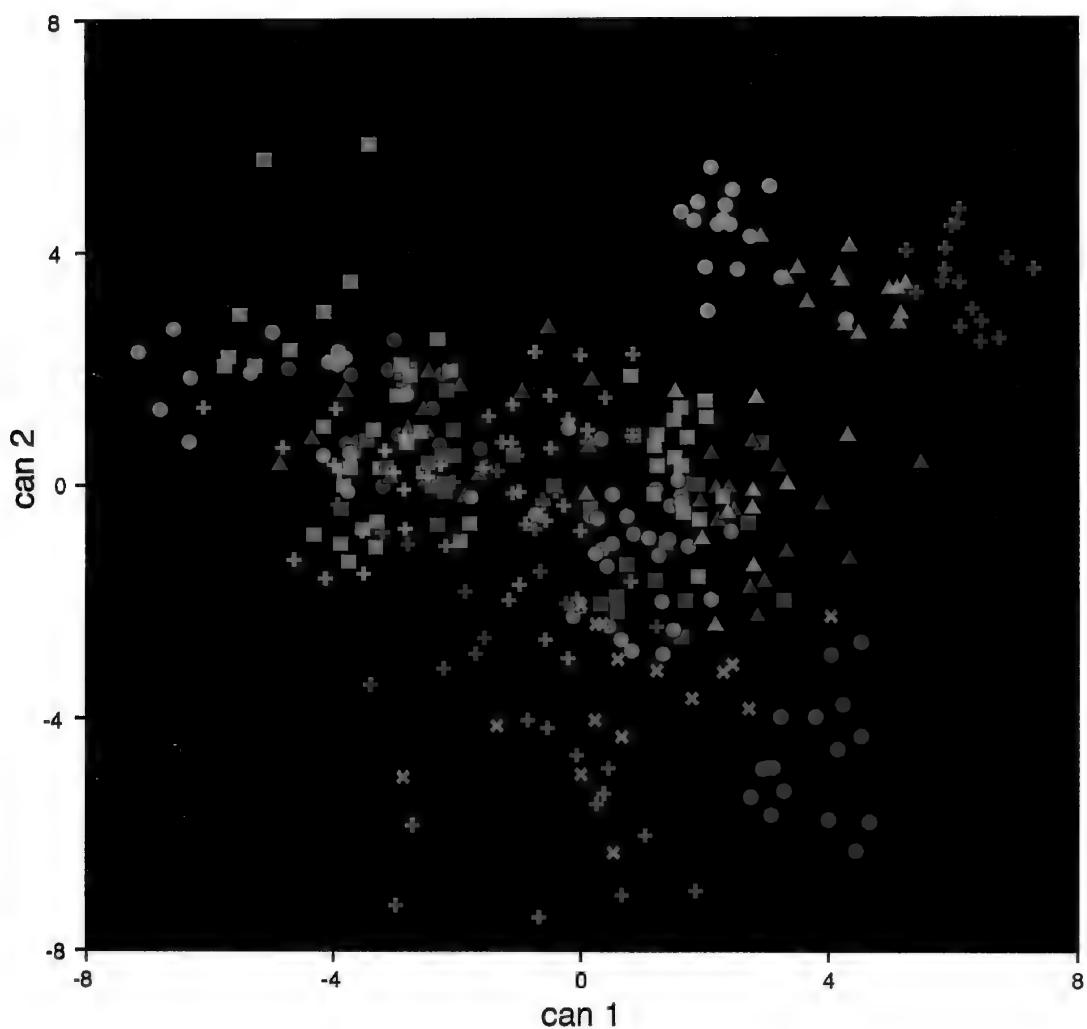
Results of all three analyses are presented in the classification matrices shown in figure 11 a-c). *C. albimarginatus*, *C. amblyrhynchos*, *C. melanopterus*, *C. wheeleri*, and *C. sorrah* have no entries in the test results of matrix 11c because they are species that were represented in the original data set by eight or fewer specimens per species. They were thus used in the creation of the "training" data set but were not numerous enough to be represented in the "test" data set.

The average discrimination achieved across species for the cross-validational analysis was 85%. This is higher than the value of 77% attained for positions E and F in the cross-validational analysis designed to investigate the relative effectiveness of different tooth positions for discrimination among species. The effectiveness of discrimination is better in the case of the data set containing only positions E and F, than it is in the data set

containing all 10 pseudotooth positions because the computed discriminant functions are not influenced by the less informative teeth from other tooth positions.

A canonical variate analysis was carried out in order to represent the differences among species graphically. The same data used in the discriminant analysis above (tooth positions E and F from the upper right jaw of the homologously aligned pseudotooth data set including eight specimens per species) were used. The plot for the first and second canonical axes is presented for all 22 species in figure 12. While it is clear that there is good separation for many species clusters, there is also considerable overlap. Much of the overlap is due to the fact that the separation among the species clusters is distributed multidimensionally (i.e., it is spread out over more than the two axes presented). In order to illustrate better the separation among clusters we need to go to higher dimensional space. This is hard to represent graphically on a printed page. One option would be to show bivariate plots of the best bivariate separation for each pair of the 22 species in the sample. This would mean presenting 231 plots. For reasons of economy, we present instead a matrix of the pairwise Mahalanobis distances between the canonical means (centroids) for each of the species clusters (fig. 13) together with a selection of plots depicting some of the most overlapping species in the two-dimensional subspace seen to maximize cluster separation (fig. 14 A-H). Note that pairs of species that show clear separation of clusters (see fig. 12) tend to have large Mahalanobis distances whereas those that are seen to overlap tend to have small Mahalanobis distances between centroids.

2. Do we have a way to distinguish the most informative tooth types from less informative tooth types when confronted with a mixture of isolated teeth from different species, as might occur in the fossil record? The previous analyses have established that it is the centrally placed teeth of the upper jaw that best distinguish among species of *Carcarhinus*. We have been unable to establish clearly which of a group of eight centrally placed teeth were optimal for the original tooth data, but have been able to narrow down the choice



- | | | |
|------------------|----------------|------------|
| ■ acronotus | ■ galapagensis | + obscurus |
| + albimarginatus | + isodon | ■ perezi |
| ● altimus | ● leucas | + plumbeus |
| ▲ amblyrhynchos | ▲ limbatus | ● porosus |
| ■ amboinensis | ■ longimanus | * sealei |
| + brachyurus | ● melanopterus | + sorrah |
| ● brevipinna | ● N. velox | ▲ wheeleri |
| ▲ falciformis | | |

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)
(1) <i>Acronotus</i>											
(2) <i>Albimarginatus</i>	30.5										
(3) <i>Altimus</i>	45.9	39.9									
(4) <i>Amblyrhynchos</i>	38.6	16.9	61.8								
(5) <i>Amboinenensis</i>	45.3	12.3	28.8	44.1							
(6) <i>Brachyurus</i>	38.0	17.5	32.5	24.9	20.5						
(7) <i>Brevipinna</i>	65.2	50.4	71.3	37.9	65.9	38.7					
(8) <i>Falciformis</i>	53.7	25.4	54.7	57.6	25.1	41.4	47.9				
(9) <i>Galapagensis</i>	33.2	15.3	16.0	38.6	7.6	15.5	55.6	34.3			
(10) <i>Isodon</i>	72.0	70.1	114.3	35.8	108.9	68.2	37.0	109.6	84.8		
(11) <i>Leucas</i>	82.4	36.6	48.7	79.8	15.2	37.0	79.1	31.0	18.7	134.0	
(12) <i>Limbatus</i>	48.6	51.1	83.2	32.8	77.7	54.8	18.0	67.5	63.8	20.1	104.8
(13) <i>Longimanus</i>	80.2	33.6	34.8	66.3	17.4	34.6	69.0	49.8	15.1	109.7	16.3
(14) <i>Melanopterus</i>	40.1	8.4	60.9	15.9	24.7	18.6	44.0	36.2	26.5	61.3	49.4
(15) <i>N. Velox</i>	14.5	16.6	34.5	25.4	36.7	25.2	66.3	53.9	25.7	71.4	71.9
(16) <i>Obscurus</i>	52.9	23.3	23.7	51.9	11.9	26.1	62.6	23.2	13.0	122.3	22.8
(17) <i>Perezi</i>	35.8	13.1	57.1	13.8	30.7	22.7	20.2	25.1	30.0	44.5	54.4
(18) <i>Plumbeus</i>	45.2	18.6	40.4	40.2	26.6	40.7	72.1	30.2	26.3	108.4	43.7
(19) <i>Porosus</i>	60.8	44.6	113.3	28.4	76.7	67.5	102.8	102.8	75.6	84.0	126.7
(20) <i>Sealei</i>	38.6	61.3	83.5	63.3	63.6	66.2	96.4	71.6	58.3	117.4	101.0
(21) <i>Sorrah</i>	71.7	39.0	94.7	48.4	47.6	61.6	118.9	79.9	60.0	144.3	90.0
(22) <i>Wheeleri</i>	24.8	10.4	55.6	4.0	33.1	21.1	38.1	43.9	29.9	37.4	65.7

	(12)	(13)	(14)	(15)	(16)	(17)	(18)	(19)	(20)	(21)
(13) <i>Longimanus</i>	82.3									
(14) <i>Melanopterus</i>	48.0	49.9								
(15) <i>N. Velox</i>	61.4	66.3	25.6							
(16) <i>Obscurus</i>	82.3	22.2	36.8	45.5						
(17) <i>Perezi</i>	26.8	53.0	7.9	31.3	35.0					
(18) <i>Plumbeus</i>	67.5	45.2	32.0	37.8	20.0	32.5				
(19) <i>Porosus</i>	75.2	117.2	34.1	54.4	88.6	45.7	52.8			
(20) <i>Sealei</i>	90.4	109.5	59.6	65.4	62.2	53.7	69.2	65.6		
(21) <i>Sorrah</i>	120.9	98.8	31.3	57.1	60.0	48.5	47.7	31.5	60.9	
(22) <i>Wheeleri</i>	29.2	57.4	14.0	18.7	45.7	12.3	35.7	33.5	55.7	52.4

Fig. 13. Matrix of pairwise Mahalanobis distances between the canonical means for each of the species clusters shown in figure 12.

←

Fig. 12. A canonical variates analysis depicting the first two canonical axes for tooth positions E and F for all 22 of the species represented in the survey. Each species is represented by eight randomly selected individuals where possible. There are thus approximately 350 teeth represented on the plot (22 different species, 8 individuals per species, 2 tooth positions per individual). Each species is depicted with a different color/symbol combination. Notice that while the clusters for a number of species are clearly separable from one another, a great many exhibit considerable overlap. Much of this overlap is due to the fact that cluster separation is distributed multidimensionally and cannot be depicted well in the two dimensions presented.

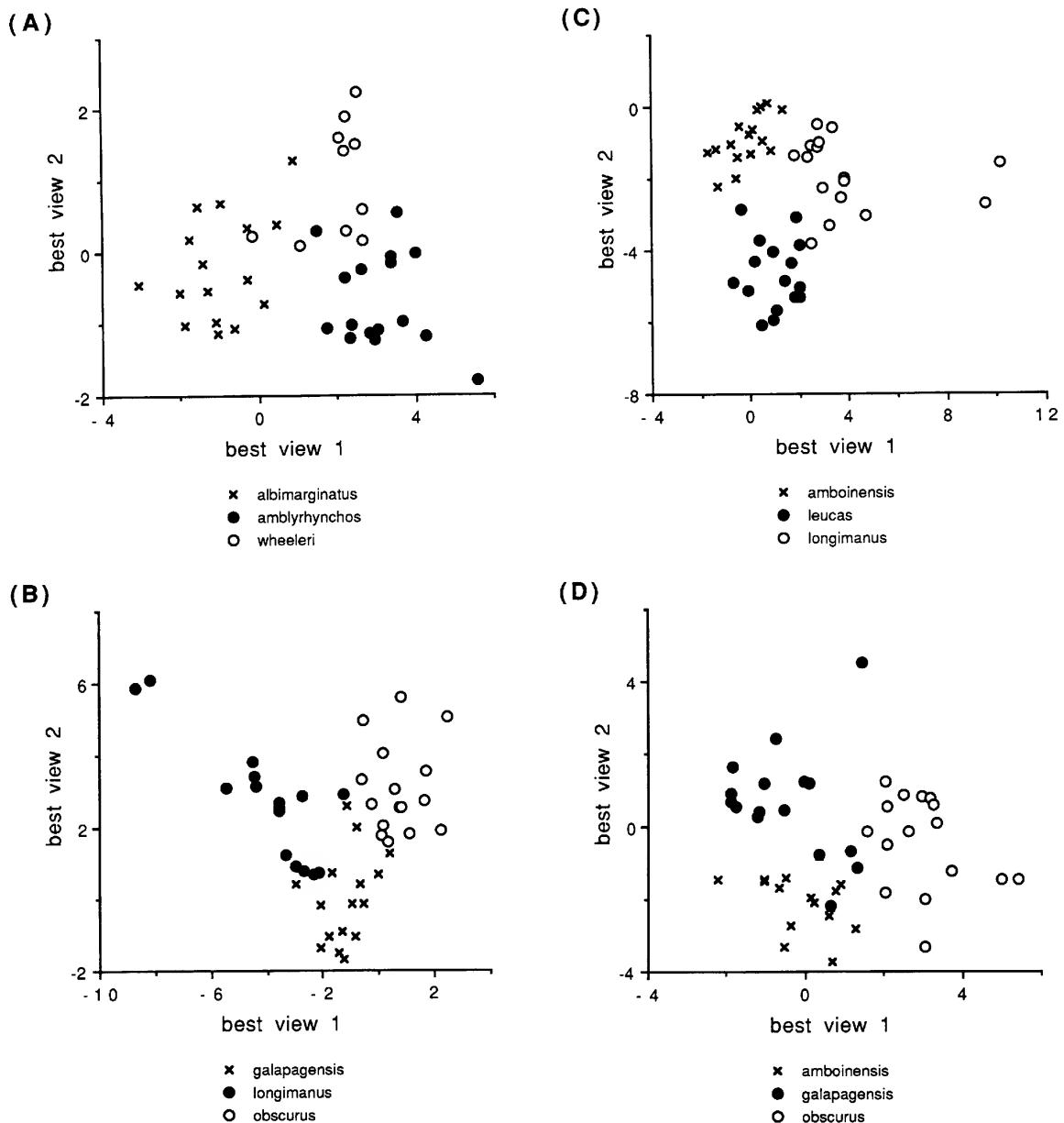


Fig. 14. Bivariate plots showing the two-dimensional view (in multidimensional space) that exhibits the best separation among species clusters. We have chosen to depict these "best views" for the species that exhibit the most overlap (or worst separation) among clusters. The "best view 1" and "best view 2" axes correspond, respectively, to "principal component 1" and "principal component 2" of the three selected species scores, for all of the canonical variates resulting from the analysis of the 22 species (see SAS routine in Appendix 2). Note that the species selected have small Mahalanobis distances between clusters (fig. 13). Best view comparisons for other species combinations would show more distinct separation among clusters.

to two positions (E and F) for the homologously aligned pseudotooth data set. It appears that the homologous realignment procedure, in standardizing all tooth series to

have the same number of teeth (10), has the effect of causing the optimal tooth position, which varies among species in the original data set, to converge on a specific region of

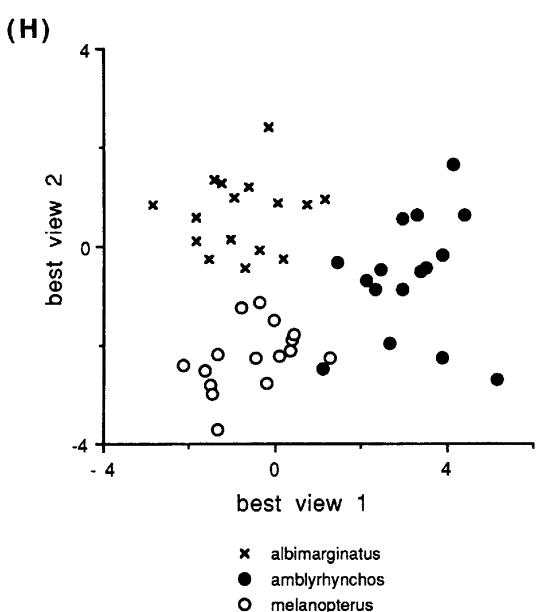
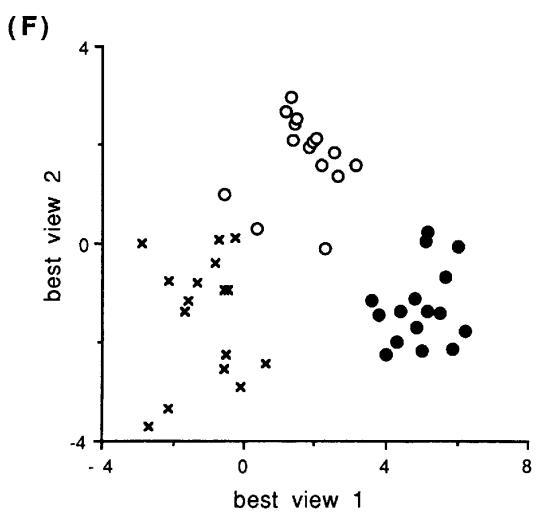
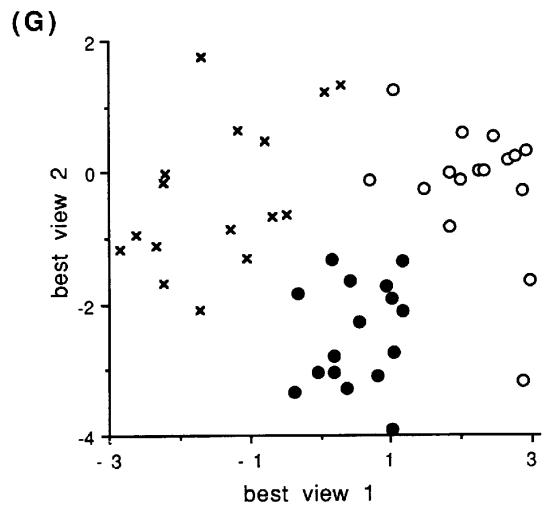
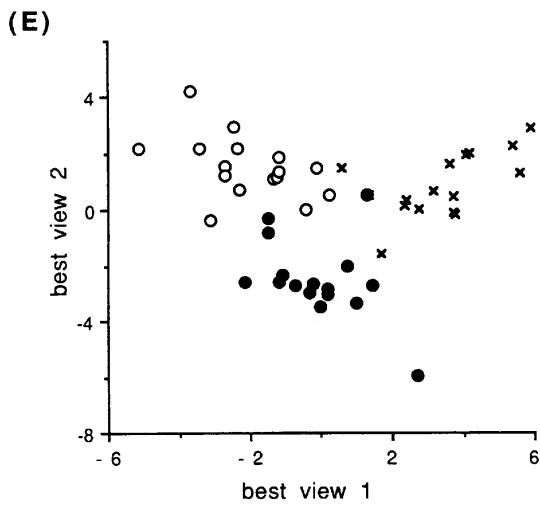


Fig. 14. Continued.

Fig. 14. Continued.

the jaw (positions E and F) in the realigned pseudotooth data set. This convergence of optimal tooth positions through realignment makes the work of distinguishing informative teeth from uninformative teeth considerably easier because all species now appear most informative at the same jaw positions. The problem of distinguishing informative from uninformative teeth can thus be recast in

terms of distinguishing the tooth positions of isolated teeth.

A discriminant analysis was carried out to assess how well tooth position could be distinguished across species. A data set was prepared in which each species was represented by eight randomly chosen individuals. The even representation of species was established so as to avoid biasing results to ac-

UPPERS																			
left					right														
A	B	C	D	E	F	G	H	I	J	A	B	C	D	E	F	G	H	I	J
UPPERS	A	90																	
	B	1	72	14	4	1	1	1	1										
	C		14	53	20	3	2	3	1	1									
	D		4	22	53	12	1	5	2										
	E		2	14	38	33	5	4	2										
	F		3	11	34	22	17	8	4	1	1								
	G		1	2	31	15	10	30	8	2	1								
	H		1		13	4	3	15	45	15	2								
	I		1		1	1	3	15	67	8									
	J							15	74										
RIGHT	A	3								90									
	B									1	72	14	4	1	1	1			
	C										14	53	20	3	2	3	1	1	
	D										4	22	53	12	1	5	2		
	E										2	14	38	33	5	4	2		
	F										3	11	34	22	17	8	4	1	1
	G										1	2	31	15	10	30	8	2	1
	H										1		13	4	3	15	45	15	2
	I										1	1		1	3	15	67	8	
	J															15	74		
LEFT	A	3									9								1
	B	1	1								1	3	1						
	C	2									2	2							
	D	1	2								1	1	1	1	1	1			1
	E		1	1							1	3		1	1				
	F		2								1	1	2	1	1				1
	G	1	1								1	3	1		1	1			
	H		1													1	3	1	
	I	1									1						4	1	
	J	1																4	
LOWERS	A	9									1	3							
	B	1	3	1							1	1							
	C	2	2									2							
	D	1	1	1	1	1					1		1	2					
	E	1	3		1	1								1	1				
	F	1	1	2	1	1					1			2					
	G	1	3	1		1	1						1	1					
	H						1	3	1						1				
	I	1						4	1										
	J							4	1										

Fig. 15. Classification matrix resulting from a quadratic discriminant analysis by jaw position and side. There are 40 categories for discrimination: 10 jaw positions (A-J) for both upper and lower jaws for both left and right sides. Rows correspond to true identities, columns to assignment categories. Correctly assigned observations thus fall into the diagonal cells of the array. Assignments are based on 16 tooth measurements taken from pseudotooth series. Each species was represented by eight randomly

										LOWERS												
left										right												
		A	B	C	D	E	F	G	H	I	J	A	B	C	D	E	F	G	H	I	J	
UPPERS	left	A										8										
		B	1	2	1								1		1	1	1					
		C		1		1								1	1			1				
		D			1										1	1						
		E		1	1																	
	right	F			1														1			
		G	1				1															
		H	1			1													1			
		I					1								1		1	2				
		J						1										1	4	5		
LOWERS	left	A	8																			
		B		1	1	1	1							1	2	1						
		C			1	1		1						1		1						
		D													1							
		E												1	1							
	right	F					1							1								
		G							1						1							
		H						1			1				1							
		I			1			1	2									1				
		J						1	4	5									1			
LOWERS	left	A	76	1					1			8								1		
		B	1	40	31	11	2	1	1					3	3	1				1		
		C	8	53	24	2	3		1	1				1	1					1		
		D	1	3	17	46	10	8	3	1	1			1	1	1						
		E	1	3	3	22	32	20	6	4	1	1		1		1						
	right	F	2	2	10	14	39	10	7	3	1		1		1	1	1	1				
		G		1	4	8	25	30	19	3	1			1	1	1			1			
		H			3	8	19	54	4	5									1	3		
		I	1	1		1	3	3	32	43	9				1		1		1	1		
		J	1		1	1	1	1	9	23	54				1				1	3		
LOWERS	left	A	8						1			76	1							1		
		B	3	3	1					1	1	40	31	11	2	1	1					
		C	1	1					1			8	53	24	2	3		1	1			
		D		1	1	1					1	3	17	46	10	8	3	1	1			
		E		1	1						1	3	3	22	32	20	6	4	1	1		
	right	F	1		1	1	1	1			2	2	10	14	39	10	7	3	1			
		G	1	1	1			1				1	4	8	25	30	19	54	4	5		
		H				1	3					3	8	19	54	4	5					
		I		1	1		1	1		1	1		1	3	3	32	43	9				
		J	1			1	3					1	1	1	1	9	23	54				

selected individuals for each of the 22 species used in the study. (Note, once again, that *C. wheeleri* and *C. sorrah* could only be represented by five and six individuals, respectively.) Observations are expressed as percentages in the matrix. Note that percentages sum to more than 100 in some cases due to rounding error.

commodate those species that were better represented in the original sample. Each of the individuals in the data set was represented by 40 pseudotooth positions, comprising 10 from the right and left sides of the top and bottom jaws. Each of these 40 pseudotooth positions was used as a category for discrimination. (Each discrimination category was thus represented by approximately 170 observations [22 species, 8 individuals per species, *C. wheeleri* and *C. sorrah* excepted].)

Initial analyses indicated that the covariance structures for the 40 pseudoposition categories were significantly different from one another, suggesting that a quadratic discriminant analysis might better discriminate among the pseudotooth-position categories than would a linear discriminant analysis. (Remember, however, that in order to realize the potential improvement associated with quadratic discriminant analysis, larger sample sizes are required—see section on Homogeneity of Covariance.) Because the sample sizes representing each category were reasonably large (170 observations per category), a quadratic discriminant analysis was used.

Results are presented in a classification matrix (fig. 15). Several important findings emerge. Most striking is the fact that the array has a large number of incorrect assignments. We have grouped these into five categories (fig. 16).

A₁) Misassignment between anteriorly placed lower right teeth and anteriorly placed lower left teeth. This can be explained by the fact that lower teeth generally are more erect (less "angled") than are upper teeth, and that anterior teeth (close to the symphysis) are more erect than centrally or posteriorly placed teeth (see fig. 7). Thus teeth on either side of the symphysis in the lower jaw, being equally erect, are similar in appearance and are thus prone to being confused. This category does not involve misassignments to the "upper E and F" positions and thus has little influence on our ability to distinguish informative from uninformative teeth.

A₂) Misassignment between anteriorly placed upper right teeth and anteriorly placed upper left teeth. This category is the counterpart to category A₁, but for the upper jaw.

Considerably fewer teeth are misassigned in this category because the upper jaw teeth are more angled on either side of the symphysis than are their lower-jaw counterparts. Indeed, the only incorrect assignments that do occur, are immediately to either side of the symphysis (position A), where upper teeth are bilaterally erect.

B) Misassignment of teeth close to the symphysis between upper and lower jaws. This includes incorrect assignments between anterior teeth from the upper right and anterior teeth from the lower left, anterior teeth from the upper right and anterior teeth from the lower right and the mirror image counterparts of both aforementioned misassignment categories. These incorrect assignments are attributable to the fact that there are a number of erect teeth found at anterior positions in the upper jaws of some species that are similar to the erect anteriorly placed lower jaw teeth of other species (and vice-versa).

C) Misassignment in the extreme posterior position between upper right and lower left teeth and between upper left and lower right teeth. This category is readily accounted for by two factors. The first is that teeth in opposite quadrants of the jaw tend to be angled in similar ways (see section on the mirror imaging procedure and also fig. 7). The second is that as one proceeds posteriorly toward the angle of the jaw, both upper and lower teeth become less distinctive (see fig. 2). This also accounts for the high incidence (80%) of misassignment by species in extreme posterior teeth. Because this type of misassignment rarely involves teeth from a lower jaw being misassigned to the upper jaw pseudotooth positions E or F, it has little bearing on our ability to distinguish informative teeth from uninformative teeth.

D) Misassignment in extreme posterior teeth between left and right sides of the lower jaw. This category can be accounted for by two contributing phenomena, the lack of distinctiveness in extreme posterior teeth coupled with the generally erect and symmetrical nature of lower jaw teeth. Posteriorly placed upper jaw teeth tend not to be misassigned between the left and right sides of the jaw, as they are less symmetrical and more angled than are their lower jaw counterparts.

E) Misassignments into adjacent tooth po-

sitions within a series in the same jaw quadrant (upper right, lower right, upper left, lower left). Most of the wrong allocations in the array fall here. This is expected, given the incrementally graded nature of monognathic tooth shape variation with tooth series in *Carcharhinus*. This type of misassignment does not seriously impede the ability to distinguish informative from noninformative teeth because teeth are rarely misassigned to positions that are more than two toothpositions away from their correct assignment.

It is important to notice that while a large percentage of teeth are not correctly assigned to their appropriate positions, the teeth that are most problematic for discriminating among species—the extreme anteriors and the extreme posteriors—are hardly ever misassigned as belonging to the upper jaw positions E and F. Restated, this means that the sample of teeth assigned to the upper jaw positions E and F contains a much more informative species-specific signal than would a randomly selected sample of teeth.

While the sample of teeth assigned to upper positions E and F includes very few extreme anterior teeth and very few extreme posterior teeth, it does include several teeth that do not originally come from positions E and F. In fact, only 57% of the observations assigned to upper jaw positions E and F are originally from these positions. However, most (29%) of the teeth incorrectly assigned to the upper jaw positions E and F are originally from tooth positions D and G, adjacent to E and F, in the same quadrant of the jaw. These adjacent positions carry a species-specific signal that is nearly as strong as that seen for positions E and F (see fig. 10, plot C). It is unlikely then, that their inclusion in the sample would strongly diminish the species-specific signal associated with positions E and F.

We have thus arrived at a reasonably satisfactory solution to the original question: Do we have a way to distinguish the most informative tooth type from less informative tooth types when confronted with a mixture of isolated teeth from different species, as might occur in the fossil record? We have an objective way to assign isolated teeth into position categories. As position is a good indicator of "informativeness" in teeth, we have an effective way to distinguish more infor-

mative teeth from less informative teeth. Furthermore, the method can realistically be applied to any isolated teeth, fossil or extant, that belong to the genus *Carcharhinus*, because the posterior probabilities for assignment are derived from a data base that encompasses nearly all of the positional variation in tooth shape seen among species of the genus.

3. How good is discrimination among species, for the teeth selected by the protocol proposed in question 2 to be most informative? Thus far, we have established that the teeth in positions E and F of the upper jaw of the homologously aligned pseudotooth data set are those that best distinguish among species of *Carcharhinus*. We have developed an objective means to distinguish most of these maximally informative teeth at positions E and F from the less informative teeth. The criterion used for selection is narrow and stringent, in that many teeth which would likely be correctly assigned to species, are excluded. However, the stringency employed ensures that those teeth least likely to be correctly assigned to species, that could also completely confound analysis, are eliminated from consideration.

The effectiveness of using a discriminant analysis by position as a criterion for selecting teeth informative for species discrimination remains to be tested empirically.

A "training" data set comprising the pseudotooth data used to address Question 2 (22 species represented by 8 individuals per species each with 40 homologously aligned pseudoteeth) was established. A discriminant analysis by jaw side and tooth position was run. A "test" data set, comprising original data (not the homologized pseudotooth data) for all those individuals not used in the "training" data set, and hereafter referred to as the "phase 1 test sample" (fig. 17a), was subjected to classification using the posterior probabilities determined from the "training" data set. All the observations from the "phase 1" test sample that were assigned to the upper right jaw pseudotooth position E and F categories were sequestered for further testing. This subsample of the "phase 1" test sample, hereafter referred to as the "phase 2 test sample," are the teeth determined by the proce-

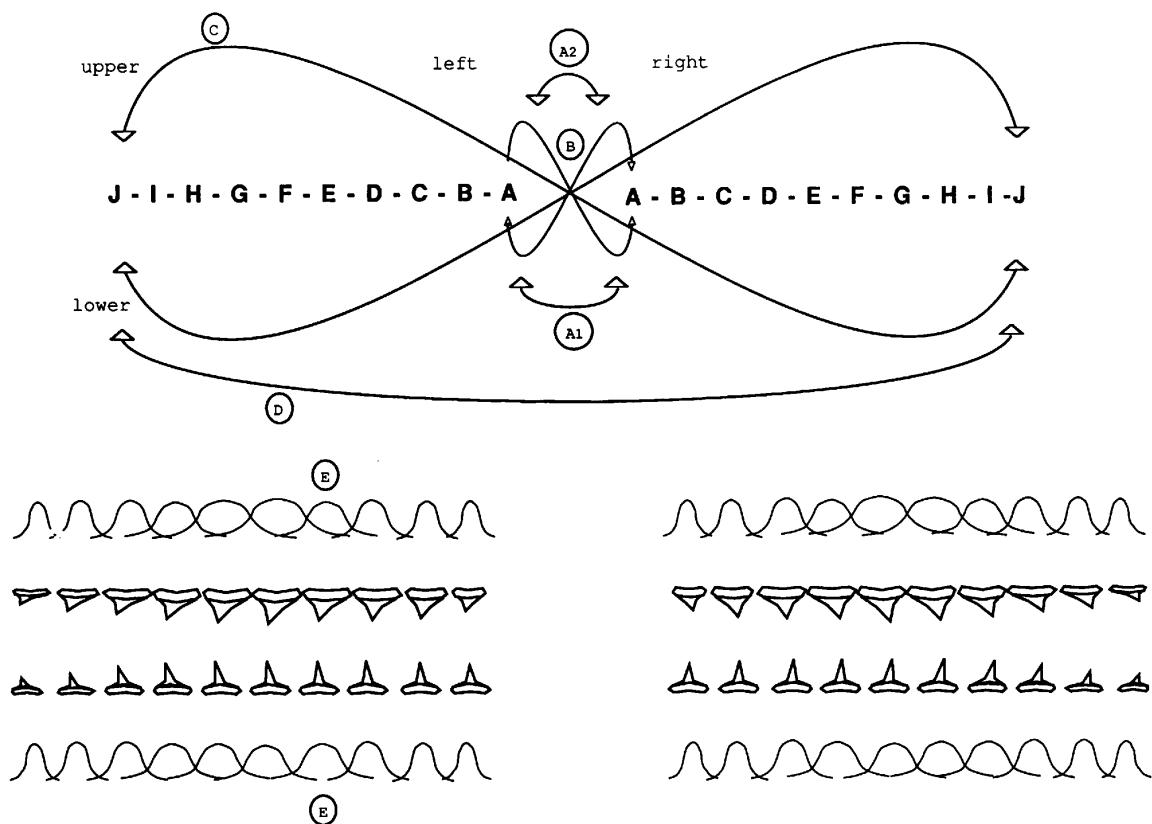


Fig. 16. Schematic diagram of a shark's jaw showing five classes of tooth misassignment, seen for the quadratic discrimination by jaw, position, and side shown in figure 15. The diagram depicts a jaw map showing the 10 pseudotooth positions A–J, for upper and lower jaws for the left and right sides. Double-headed arrows point to regions that are frequently misassigned. Thus, the arrows labeled A depict the class of misassignments whereby tooth positions close to the symphysis within the lower jaw (A_1) or within the upper jaw (A_2) are wrongly identified as belonging to the other side of the jaw. The B arrows depict the class of misassignments whereby tooth positions close to the symphysis are wrongly allocated to anterior tooth positions in the opposite quadrant of the jaw. Hence, upper left anterior teeth are misassigned as lower right anterior teeth, and vice versa, whereas upper right anterior teeth are misassigned as lower left anterior teeth, and vice versa. Misassignment category E refers to the situation whereby teeth from nearby (most commonly, adjacent) tooth positions in the same quadrant of the jaw are wrongly assigned. We have depicted this as a separate jaw map with tooth positions showing their corresponding bell-shaped curve distributions overlapping between positions. Refer to text for further explanation of each misassignment category.

dure to carry the optimal species specific signal in the "test" data. The compositional breakdown of the actual tooth positions represented in this phase 2 test sample is depicted as a histogram in figure 17b. Several things should be noted:

1. Teeth from a large number of positions are represented. Much of this is due to the fact that the "test" data are original rather than homologously aligned, and therefore

necessarily include a greater variety of tooth positions. (Remember that positions E and F of the homologously aligned data correspond to a wider variety of tooth positions in the original data.) However, it is also true that some of the variation in tooth position is due to the imperfect performance of the discriminant analysis.

2. The modal tooth positions selected by the procedure are positions 7 and 8 of the

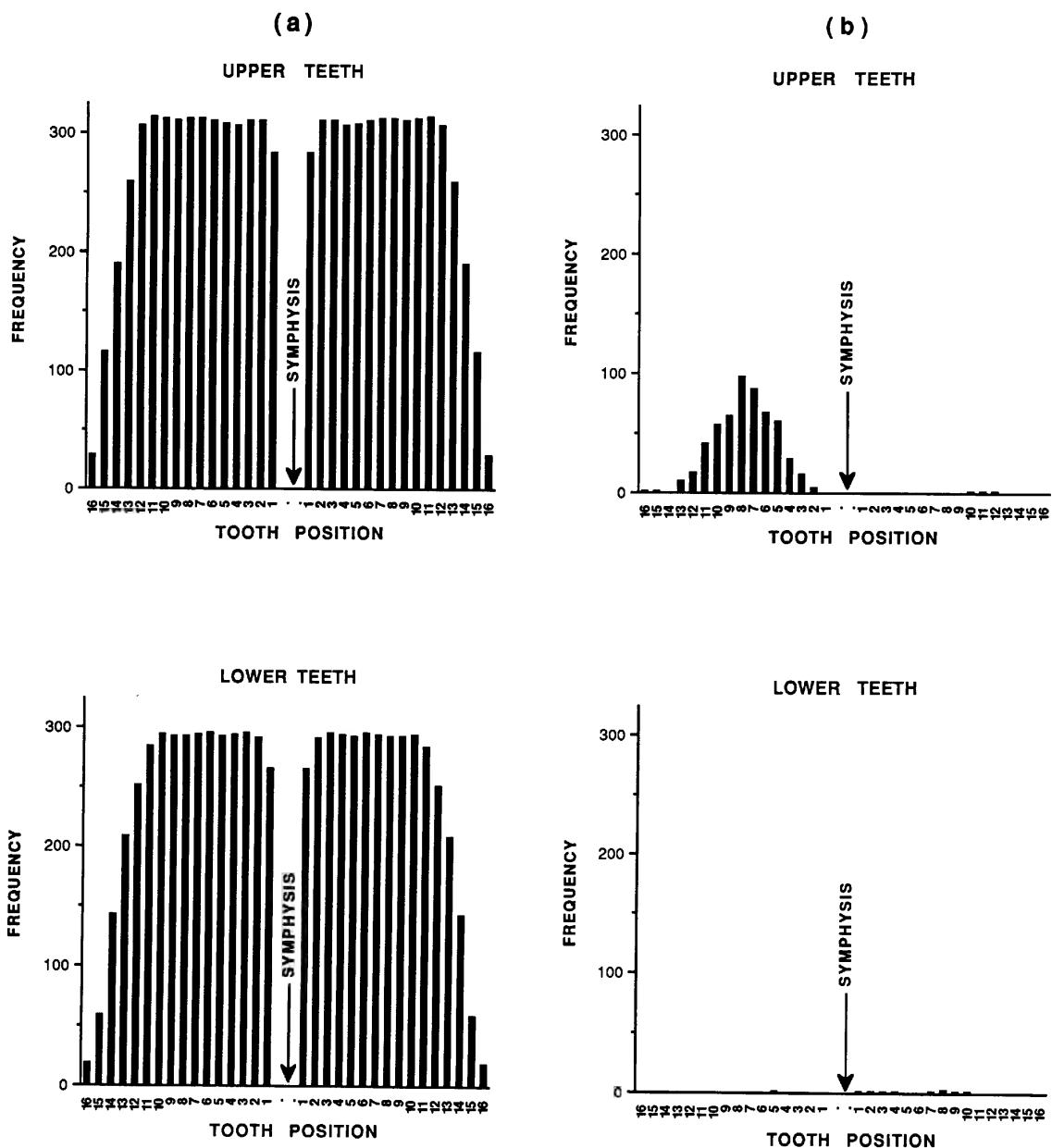


Fig. 17. a. Histograms of tooth positions represented in the phase 1 test sample, comprising observations derived from individuals not used to establish the discriminant functions by jaw, positions and side. Note that 16 tooth position categories are present because the data correspond to original data rather than to homologously aligned pseudotooth data. Accordingly, the posteriorly placed tooth position categories are less well represented than are other tooth position categories (because most species tend not to have more than 13 tooth positions per quadrant). b. Histograms of tooth positions represented in the phase 2 test sample. This sample represents those teeth in the phase 1 test sample (see fig. 17a) that were assigned to pseudotooth positions E and F. Assignments were based on discriminant functions derived from the "training" data set. Refer to text for further details.

	acronotus	albimarginatus	altimus	amblyrhynchos	amboinensis	brachyurus	brevipinna	falciformis	galapagensis	isodon	leucas	limbatus	longimanus	melanopterus	obscurus	perezi	plumbeus	porosus	sealei	sorrah	velox	wheeleri
acronotus	38 80.85				1				1			1							1	4	1	
albimarginatus																						
altimus			23 82.14						1	1									1	2		
amblyrhynchos																						
amboinensis		4		24 84.86	1				4			1	1		1					1		
brachyurus					63 88.73	1			2		1			3							1	
brevipinna						18 69.23						3			4					1		
falciformis	3	1	1	3	1		56 65.12	2						6	4	6		1			2	
galapagensis					3				15 60				4	1								
isodon									6 100													
leucas				9	2					14 48.28		4										
limbatus						2			2		14 58.33				3		1		1		1	
longimanus		2		1	3			3				9 47.37	1									
melanopterus																						
obscurus					2				5	1	1			13 50		3		1				
perezi						1								2 40						2		
plumbeus	1	3	1			1		4							41 73.21							
porosus				2							1				28 71.79		1		1			
sealei				1											14 93.33							
sorrah																						
velox	2				1						1	1						1	20 71.43	2		
wheeleri																						

Fig. 18. Classification matrix resulting from a posteriori assignment of observations in the phase 2 test sample (fig. 17b) to species categories based on linear discriminant functions of 16 tooth-shape measurements. Discriminant functions were computed from a "training" data set comprising pseudotooth positions D, E, F and G for 22 species. Each species in the "training" data set was represented by 8 individuals (*C. wheeleri* and *C. sorrah* excepted). Note that only 17 species were numerous enough in the original data set to be represented in the phase 2 test sample. See text for details.

original data. This closely corresponds to positions E and F of the homologously aligned pseudotooth data set.

3. Very few lower teeth are included in the sample. It is interesting to note that the 11 that are included all come from the opposite quad-

rant of the jaw (i.e., the lower left quadrant) as might be predicted from the way in which their enameloid crowns are angled (see fig. 7).

4. Only three teeth from the upper left-hand side were selected by the procedure.

5. Very few teeth from the extreme anterior

or the extreme posterior of any jaw are included.

6. A number of species are not represented. This is due to the fact that they were not numerous enough in the original data set to be included in both the "test" and the "training" data sets.

Teeth from upper positions D, E, F, and G of the "training" data set (homologously aligned pseudotooth data set) were subsequently used to create a model for discrimination among species. These four positions were chosen because they correspond to the majority of tooth positions represented in the phase 2 test sample (see fig. 17b). The observations in the phase 2 test sample were then assigned to species using the posterior probabilities computed for positions D, E, F, and G of the "training" (pseudotooth) data set.

Results of this discriminant analysis are presented in the classification matrix shown in figure 18. The percentage of correctly assigned observations in the array varied from 40 to 100% and averaged 70% across species. Note that only 17 species were numerous enough in the original data set to be represented in the phase 2 test sample. Almost all misassigned observations were to species whose tooth shapes are similar (see fig. 2). This is a particularly encouraging result because it supports our intuition that if teeth are misassigned, they should be misassigned to groups that are similar in appearance. In essence, it suggests that the linear measurements chosen reflect perceived shape similarities and differences among teeth.

The percentage of teeth that are misassigned is appreciably higher than that seen for the linear discriminant analysis carried out for the teeth of upper positions E and F of the pseudotooth data set carried out for Question 1 (see fig. 11c). This is because teeth were selected a priori from upper positions E and F for Question 1. The phase 2 test sample, by contrast, was selected through a posteriori allocation by discriminant analysis. Since this allocation procedure is based on probabilities of correct identities, it inevitably includes occasional teeth from other tooth positions. The added variation in tooth position translates into decreased assignment accuracy when a discriminant analysis by species is carried out.

CONCLUSIONS

We have presented a series of tests to determine which teeth are most useful for distinguishing among species. We have developed a protocol that allows us to select objectively from a loose collection of unidentified isolated teeth (about which nothing is known but that they belong to the genus *Carcharhinus*) those teeth that are most likely to be useful for distinguishing among species. We have rigorously tested the effectiveness of the selection protocol using an unseen "test" data set and found the procedure to be satisfactory for isolated teeth from living sharks. We have reason to believe that the procedure should also be effective for selecting those isolated teeth from the fossil record which are most distinctive among species.

The application of the protocol to isolated teeth in the fossil record requires that two assumptions be made:

1. That tooth shape variation by position and by jaw is the same in fossil species of *Carcharhinus* as it is in living forms. This assumption can be justified by noting that all extant members of the genus exhibit similar monognathic and dignathic trends (refer to fig. 2). If fossil members of the genus exhibited a different trend, it would be necessary to invoke convergence toward the same kind of monognathic and dignathic heterodonty in 30 extant taxa. There is no a priori reason to invoke such an assertion.

2. That fossil taxa can be distinguished by the shape of their teeth. It is hard to substantiate this claim empirically. However, to quote Garrick (1982), "If one takes an overview of shark systematics in general, the best single feature that could be cited for determining similarities and differences between taxa at all levels, but perhaps predominantly at the generic level, is the shape of the teeth." Given this, and the fact that the fossil record of shark teeth exhibits a wide variety of tooth shapes, it is probably reasonable to assume that the fossil species of *Carcharhinus*, like their living counterparts, can be distinguished by their tooth shapes.

We feel that the protocol outlined in this study will be effective for separating isolated fossil *Carcharhinus* teeth that are maximally distinctive among species, from those that are less informative. This will make it po-

tentially possible to trace *Carcharhinus* species lineages at successive geological horizons through the fossil record.

ACKNOWLEDGMENTS

We thank all those who have assisted with this project in various ways over the past eight years. We particularly thank the commercial fishermen and scientists who allowed Gavin Naylor to accompany them fishing or who collected specimens on our behalf. They are: from the east coast of North America, D. De Maria, R. Bakey, E. Sanders, N. Sanders, S. Poston, J. Casey, H. Pratt, J. Castro, S. Branstetter, J. Musick, and J. Colvocoresis; from Hawaii: E. Schellenburger, S. Kaiser and M. Suiso; from the Red Sea: A. Sulliman and "Muhammed"; from the Philippines: the villagers and fishermen of Arena Blanco, Mindanao; from South Africa: G. Cliff, P. Cowley, and the shark net inspection crews of the Natal Sharks Board.

We thank G. Cliff, P. Heemstra, L. J. V. Compagno, J. Castro, C. Schottman, and D. De Maria for graciously making their homes available to Gavin Naylor as a base from which to carry out fieldwork. We offer special thanks to Rebecca Naylor and to Sophie Dyson for the six weeks they spent meticulously extracting, cleaning, labeling and cataloging 13,000 shark teeth under adverse conditions, to Dr. Walter Barton Elvers for his unflagging patience and rigor in measuring the majority of the teeth used in the study, to Pat Wynne for her excellent line drawings, to David Bay

for the black and white photographs, and to Matt Doty of Strong Productions Ltd., Cedar Rapids, Iowa for reproduction of the color plate.

Others who generously provided either direct assistance or advice were R. Apilado, "Mungpert" and D. Cadra (Philippines); J. Parrish and Sea Life Park (Hawaii), A. J. M. Naylor, W. I. Naylor, and P. Showers (Sierra Leone); R. Fox, D. Doubilet and H. Fraise (Australia); L. Compagno, P. Heemstra, G. Cliff, N. Kistnasamy, the staff at the J. L. B. Smith Institute (S. Africa); M. Doty, L. Cohen, T. Bowman (Belize), S. Blum, R. Shipp, J. Dendo, G. Nelson, L. Abele, V. Springer, J. Maisey, R. Purdy, G. Hubell, G. Burgess, E. Clark, D. Gill, G. Vermeij, M. Novacek, J. Ott, E. Silverfine, D. Carr, J. Jibrin, S. Wilkes, S. Fitzgerald, D. Chipman, and E. Knurek (U.S.A.).

We are particularly grateful to Louise Roth for her insight and advice on the comparison of serial homologs. We thank Philip Gingerich, John Maisey, Erik Mattison, Richard Reyment, Mike Foote, and Jim Rohlf for constructive criticism and editorial improvement of earlier drafts of the manuscript.

Financial support for this project was provided by the W. I. N. Foundation, the University of Maryland Foundation, the University of Maryland Computer Science Center, the City University of New York Computer Science Center, D. Shen, the National Science Foundation, (grant BSR 87-08121 to G. J. Vermeij), the Lerner Gray Fund for Marine Research, and The American Museum of Natural History.

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APPENDIX 1
Material Examined

Species	Sex	TL ^a	U ^b	L ^c	Locality	ID ^d
ACRONOTUS	F	78	12	12	454791,60516.3 (LORAN), S. Carolina, U.S.A.	391
ACRONOTUS	F	81	11	10	Ponce Inlet, Florida, U.S.A.	460
ACRONOTUS	F	87	11	11	Ponce Inlet, Florida, U.S.A.	459
ACRONOTUS	F	114	12	-	Mayport, Jacksonville, Florida, U.S.A.	442
ACRONOTUS	F	115	12	10	Dauphin Is., Alabama, U.S.A.	151
ACRONOTUS	F	124	12	10	Marathon, Florida Keys, Florida, U.S.A.	470
ACRONOTUS	F	126	12	11	Bulls Bay, nr. Charleston, S. Carolina, U.S.A.	400
ACRONOTUS	F	134	12	12	Mayport, Jacksonville, Florida, U.S.A.	435
ACRONOTUS	F	138	12	11	Bulls Bay, nr. Charleston, S. Carolina, U.S.A.	379
ACRONOTUS	F	141	12	11	Bulls Bay, nr. Charleston, S. Carolina, U.S.A.	381
ACRONOTUS	M	-	11	11	Bulls Bay, nr. Charleston, S. Carolina, U.S.A.	374
ACRONOTUS	M	-	12	11	Bulls Bay, nr. Charleston, S. Carolina, U.S.A.	389
ACRONOTUS	M	87	12	11	454791,60516.3 (LORAN), S. Carolina, U.S.A.	372
ACRONOTUS	M	98	12	11	St. Andrew's Bay, Panama City, Florida, U.S.A.	78
ACRONOTUS	M	117	12	11	Bulls Bay, nr. Charleston, S. Carolina, U.S.A.	382
ACRONOTUS	M	118	12	11	Bulls Bay, nr. Charleston, S. Carolina, U.S.A.	386
ACRONOTUS	M	123	12	11	Bulls Bay, nr. Charleston, S. Carolina, U.S.A.	383
ACRONOTUS	M	123	11	11	Bulls Bay, nr. Charleston, S. Carolina, U.S.A.	388
ACRONOTUS	M	124	12	11	Bulls Bay, nr. Charleston, S. Carolina, U.S.A.	404
ACRONOTUS	M	125	12	11	Bulls Bay, nr. Charleston, S. Carolina, U.S.A.	403
ACRONOTUS	M	126	12	11	Bulls Bay, nr. Charleston, S. Carolina, U.S.A.	387
ACRONOTUS	M	130	12	11	Bulls Bay, nr. Charleston, S. Carolina, U.S.A.	401
ACRONOTUS	M	132	12	11	Bulls Bay, nr. Charleston, S. Carolina, U.S.A.	384
ACRONOTUS	M	132	12	11	Bulls Bay, nr. Charleston, S. Carolina, U.S.A.	385
ACRONOTUS	M	136	12	11	Bulls Bay, nr. Charleston, S. Carolina, U.S.A.	402
ALBIMARGINATUS	?	-	12	12	Oro pt. Mariana, J. L. B. Smith Inst. (#006543)	823
ALBIMARGINATUS	F	84	13	11	Socorro Island, E. Pacific (L.J.V.C. #0214), MEXICO	841
ALBIMARGINATUS	F	92	13	12	Mercedes, Camarines Norte, PHILIPPINES	287
ALBIMARGINATUS	F	266	13	12	J. L. B. Smith Inst. (#006547), MAURITIUS	822
ALBIMARGINATUS	M	-	13	12	J. L. B. Smith Inst. (#006542), MAURITIUS	824
ALBIMARGINATUS	M	76	13	12	J. L. B. Smith Inst. (#006544), MOZAMBIQUE	825
ALBIMARGINATUS	M	78	13	11	Cape San Lucas, E. Pacific (L.J.V.C. #0208), MEXICO	840
ALBIMARGINATUS	M	79	12	-	Socorro Island, E. Pacific (L.J.V.C. #0204), MEXICO	839
ALTIMUS	F	98	14	14	J. L. B. Smith Inst. (#006310), S. AFRICA	719
ALTIMUS	F	103	14	14	J. L. B. Smith Inst. (#006305), S. AFRICA	715
ALTIMUS	F	110	15	14	J. L. B. Smith Inst. (#006309), S. AFRICA	720
ALTIMUS	F	116	-	14	J. L. B. Smith Inst. (#006303), S. AFRICA	736
ALTIMUS	F	119	14	14	J. L. B. Smith Inst. (#006308), S. AFRICA	725
ALTIMUS	F	120	14	14	J. L. B. Smith Inst. (#006296), S. AFRICA	726
ALTIMUS	F	121	14	14	J. L. B. Smith Inst. (#006307), S. AFRICA	735
ALTIMUS	F	123	14	14	J. L. B. Smith Inst. (#006302), S. AFRICA	717
ALTIMUS	F	125	14	14	J. L. B. Smith Inst. (#006304), S. AFRICA	723
ALTIMUS	F	130	14	14	J. L. B. Smith Inst. (#006313), S. AFRICA	714
ALTIMUS	F	134	14	14	J. L. B. Smith Inst. (#006297), S. AFRICA	728
ALTIMUS	F	136	15	14	J. L. B. Smith Inst. (#006292), S. AFRICA	731
ALTIMUS	F	139	15	15	J. L. B. Smith Inst. (#006301), S. AFRICA	729
ALTIMUS	F	141	15	15	J. L. B. Smith Inst. (#006294), S. AFRICA	727
ALTIMUS	M	91	14	15	J. L. B. Smith Inst. (#006316), S. AFRICA	718
ALTIMUS	M	108	15	13	J. L. B. Smith Inst. (#006315), S. AFRICA	722
ALTIMUS	M	120	14	14	J. L. B. Smith Inst. (#006314), S. AFRICA	721
ALTIMUS	M	120	14	13	J. L. B. Smith Inst. (#006306), S. AFRICA	724
ALTIMUS	M	128	15	14	J. L. B. Smith Inst. (#006300), S. AFRICA	732
ALTIMUS	M	128	15	14	J. L. B. Smith Inst. (#006299), S. AFRICA	734
ALTIMUS	M	130	14	15	J. L. B. Smith Inst. (#006311), S. AFRICA	730
ALTIMUS	M	134	15	15	J. L. B. Smith Inst. (#006298), S. AFRICA	716
ALTIMUS	M	139	15	14	J. L. B. Smith Inst. (#006295), S. AFRICA	737
ALTIMUS	M	159	15	14	J. L. B. Smith Inst. (#006293), S. AFRICA	733
AMBLYRHYNCHOS	?	-	14	14	Nihoa Island (N.W. Hawaiian Islands), U.S.A.	550

APPENDIX 1—(Continued)

Species	Sex	TL ^a	U ^b	L ^c	Locality	ID ^d
AMBLYRHYNCHOS	F	62	13	-	Tumalutab Is., Zamboanga City, Mindanao, PHILIPPINES	328
AMBLYRHYNCHOS	F	77	14	12	Tumalutab Is., Zamboanga City, Mindanao, PHILIPPINES	327
AMBLYRHYNCHOS	F	99	14	12	Mercedes, Camarines Norte, PHILIPPINES	289
AMBLYRHYNCHOS	F	154	14	14	Nihoa Island (N.W. Hawaiian Islands), U.S.A.	545
AMBLYRHYNCHOS	M	101	13	13	Mercedes, Camarines Norte, PHILIPPINES	288
AMBLYRHYNCHOS	M	145	13	12	Nihoa Island (N.W. Hawaiian Islands), U.S.A.	549
AMBLYRHYNCHOS	M	179	13	13	Nihoa Island (N.W. Hawaiian Islands), U.S.A.	547
AMBOINENSIS	F	132	12	11	J. L. B. Smith Inst. (#006321), S. AFRICA	764
AMBOINENSIS	F	139	12	12	J. L. B. Smith Inst. (#006326), S. AFRICA	765
AMBOINENSIS	F	140	12	11	J. L. B. Smith Inst. (#006317), S. AFRICA	766
AMBOINENSIS	F	142	-	11	J. L. B. Smith Inst. (#006334), S. AFRICA	769
AMBOINENSIS	F	147	12	12	J. L. B. Smith Inst. (#006335), S. AFRICA	770
AMBOINENSIS	F	150	12	11	J. L. B. Smith Inst. (#006330), S. AFRICA	772
AMBOINENSIS	F	158	12	11	J. L. B. Smith Inst. (#006329), S. AFRICA	775
AMBOINENSIS	F	182	12	11	J. L. B. Smith Inst. (#006333), S. AFRICA	779
AMBOINENSIS	F	184	12	12	J. L. B. Smith Inst. (#006328), S. AFRICA	781
AMBOINENSIS	F	206	12	11	Natal Sharks Board, S. AFRICA	867
AMBOINENSIS	F	223	12	-	J. L. B. Smith Inst. (#006331), S. AFRICA	783
AMBOINENSIS	M	-	13	12	J. L. B. Smith Inst. (#006319), S. AFRICA	780
AMBOINENSIS	M	132	-	11	J. L. B. Smith Inst. (#006320), S. AFRICA	784
AMBOINENSIS	M	141	12	12	J. L. B. Smith Inst. (#006322), S. AFRICA	767
AMBOINENSIS	M	141	12	11	J. L. B. Smith Inst. (#006327), S. AFRICA	768
AMBOINENSIS	M	149	12	-	J. L. B. Smith Inst. (#006325), S. AFRICA	771
AMBOINENSIS	M	153	12	11	J. L. B. Smith Inst. (#006323), S. AFRICA	773
AMBOINENSIS	M	157	12	11	J. L. B. Smith Inst. (#006336), S. AFRICA	774
AMBOINENSIS	M	160	12	12	J. L. B. Smith Inst. (#006337), S. AFRICA	776
AMBOINENSIS	M	166	12	11	J. L. B. Smith Inst. (#006318), S. AFRICA	778
AMBOINENSIS	M	196	12	12	J. L. B. Smith Inst. (#006324), S. AFRICA	782
BRACHYURUS	F	80	15	-	J. L. B. Smith Inst. (#006356), S. AFRICA	705
BRACHYURUS	F	123	15	14	J. L. B. Smith Inst. (#006344), S. AFRICA	700
BRACHYURUS	F	131	15	-	J. L. B. Smith Inst. (#006343), S. AFRICA	697
BRACHYURUS	F	157	15	14	J. L. B. Smith Inst. (#006341), S. AFRICA	701
BRACHYURUS	F	169	15	14	J. L. B. Smith Inst. (#006360), S. AFRICA	696
BRACHYURUS	F	199	15	14	J. L. B. Smith Inst. (#006350), S. AFRICA	693
BRACHYURUS	F	202	15	14	J. L. B. Smith Inst. (#006346), S. AFRICA	682
BRACHYURUS	F	202	15	14	J. L. B. Smith Inst. (#006345), S. AFRICA	695
BRACHYURUS	F	220	15	14	J. L. B. Smith Inst. (#006339), S. AFRICA	683
BRACHYURUS	F	256	16	15	J. L. B. Smith Inst. (#006369), S. AFRICA	685
BRACHYURUS	F	262	15	14	J. L. B. Smith Inst. (#006363), S. AFRICA	689
BRACHYURUS	F	262	15	14	J. L. B. Smith Inst. (#006368), S. AFRICA	698
BRACHYURUS	M	77	15	14	Port Alfred, Cape Province, S. AFRICA	710
BRACHYURUS	M	89	15	-	J. L. B. Smith Inst. (#006353), S. AFRICA	706
BRACHYURUS	M	128	15	14	J. L. B. Smith Inst. (#006362), S. AFRICA	709
BRACHYURUS	M	138	15	14	J. L. B. Smith Inst. (#006355), S. AFRICA	684
BRACHYURUS	M	139	-	14	J. L. B. Smith Inst. (#006359), S. AFRICA	694
BRACHYURUS	M	143	-	14	J. L. B. Smith Inst. (#006366), S. AFRICA	704
BRACHYURUS	M	143	15	14	J. L. B. Smith Inst. (#006342), S. AFRICA	708
BRACHYURUS	M	149	15	14	J. L. B. Smith Inst. (#006354), S. AFRICA	703
BRACHYURUS	M	152	15	14	J. L. B. Smith Inst. (#006365), S. AFRICA	707
BRACHYURUS	M	164	15	14	J. L. B. Smith Inst. (#006349), S. AFRICA	692
BRACHYURUS	M	196	15	15	J. L. B. Smith Inst. (#006348), S. AFRICA	702
BRACHYURUS	M	211	15	14	J. L. B. Smith Inst. (#006358), S. AFRICA	688
BRACHYURUS	M	213	15	14	J. L. B. Smith Inst. (#006357), S. AFRICA	690
BRACHYURUS	M	219	15	14	J. L. B. Smith Inst. (#006347), S. AFRICA	681
BRACHYURUS	M	220	15	15	J. L. B. Smith Inst. (#006352), S. AFRICA	686
BRACHYURUS	M	230	15	14	J. L. B. Smith Inst. (#006367), S. AFRICA	699
BRACHYURUS	M	233	16	15	J. L. B. Smith Inst. (#006351), S. AFRICA	691
BRACHYURUS	M	262	15	14	J. L. B. Smith Inst. (#006340), S. AFRICA	680

APPENDIX 1—(Continued)

Species	Sex	TL ^a	U ^b	L ^c	Locality	ID ^d
BRACHYURUS	M	266	15	14	J. L. B. Smith Inst. (#006361), S. AFRICA	679
BRACHYURUS	M	295	15	15	Mzamba, Natal Coast, S. AFRICA	636
BREVIPINNA	F	79	16	-	Visayan Sea (Cebu City mkt.), PHILIPPINES	326
BREVIPINNA	F	86	15	15	Freetown (Sierra fisheries by catch), SIERRA LEONE	190
BREVIPINNA	F	95	15	-	Fort Morgan, Alabama, U.S.A.	6510
BREVIPINNA	F	96	16	16	Freetown (Sierra fisheries by catch), SIERRA LEONE	193
BREVIPINNA	F	104	15	15	Dauphin Is., Alabama, U.S.A.	145
BREVIPINNA	F	150	16	-	Dauphin Is., Alabama, U.S.A.	6513
BREVIPINNA	F	150	16	-	Dauphin Is., Alabama, U.S.A.	6514
BREVIPINNA	F	163	16	15	Mobile Bay, Alabama, U.S.A.	6515
BREVIPINNA	F	170	15	-	5 mi S.W. Mobile Buoy, Alabama, U.S.A.	6496
BREVIPINNA	F	176	16	15	Pensacola, Florida, U.S.A.	6516
BREVIPINNA	F	191	15	16	25 mi S.W. Mobile Buoy, Alabama, U.S.A.	6495
BREVIPINNA	F	203	16	16	Dauphin Is., Alabama, U.S.A.	6498
BREVIPINNA	F	212	16	15	25 mi S.W. Mobile buoy, Alabama, U.S.A.	6493
BREVIPINNA	F	216	16	16	Ponce Inlet, Florida, U.S.A.	452
BREVIPINNA	F	227	16	15	Ponce Inlet, Florida, U.S.A.	461
BREVIPINNA	F	233	16	15	Freetown (Sierra fisheries by catch) SIERRA LEONE	208
BREVIPINNA	M	71	16	15	Turtle Islands, Sulu Sea (Navotas mkt.) PHILIPPINES	271
BREVIPINNA	M	72	16	16	Navotas mkt., Manila (from Palawan), PHILIPPINES	356
BREVIPINNA	M	74	16	15	Navotas mkt., Manila (from Palawan), PHILIPPINES	355
BREVIPINNA	M	78	-	15	Navotas mkt., Manila (from Palawan), PHILIPPINES	354
BREVIPINNA	M	82	16	15	Navotas mkt., Manila (from Palawan), PHILIPPINES	357
BREVIPINNA	M	83	15	-	Turtle Islands, Sulu Sea (Navotas mkt.) PHILIPPINES	311
BREVIPINNA	M	85	16	16	Freetown (Sierra fisheries by catch) SIERRA LEONE	221
BREVIPINNA	M	86	15	15	Freetown (Sierra fisheries by catch) SIERRA LEONE	200
BREVIPINNA	M	105	15	-	Dauphin Is., Alabama, U.S.A.	152
BREVIPINNA	M	159	16	15	Ponce Inlet, Florida, U.S.A.	445
BREVIPINNA	M	177	16	15	Dauphin Is., Alabama, U.S.A.	144
BREVIPINNA	M	203	16	16	Ponce Inlet, Florida, U.S.A.	450
FALCIFORMIS	?	-	15	-	Moro Gulf, S. of Mindanao, PHILIPPINES	336
FALCIFORMIS	?	-	16	15	Moro Gulf, S. of Mindanao, PHILIPPINES	344
FALCIFORMIS	?	-	16	16	Moro Gulf, S. of Mindanao, PHILIPPINES	345
FALCIFORMIS	?	167	16	16	Moro Gulf, S. of Mindanao, PHILIPPINES	346
FALCIFORMIS	?	192	16	16	Moro Gulf, S. of Mindanao, PHILIPPINES	332
FALCIFORMIS	?	195	15	15	Moro Gulf, S. of Mindanao, PHILIPPINES	334
FALCIFORMIS	?	198	16	15	Moro Gulf, S. of Mindanao, PHILIPPINES	335
FALCIFORMIS	?	200	16	16	Moro Gulf, S. of Mindanao, PHILIPPINES	330
FALCIFORMIS	?	205	15	15	Moro Gulf, S. of Mindanao, PHILIPPINES	349
FALCIFORMIS	?	208	16	16	Moro Gulf, S. of Mindanao, PHILIPPINES	329
FALCIFORMIS	?	208	16	16	Moro Gulf, S. of Mindanao, PHILIPPINES	341
FALCIFORMIS	?	211	16	16	Moro Gulf, S. of Mindanao, PHILIPPINES	342
FALCIFORMIS	?	216	16	15	Moro Gulf, S. of Mindanao, PHILIPPINES	333
FALCIFORMIS	?	217	15	15	Moro Gulf, S. of Mindanao, PHILIPPINES	347
FALCIFORMIS	?	219	16	16	Moro Gulf, S. of Mindanao, PHILIPPINES	348
FALCIFORMIS	?	224	16	16	Moro Gulf, S. of Mindanao, PHILIPPINES	331
FALCIFORMIS	F	67	15	-	Port of Spain fish market, TRINIDAD	515
FALCIFORMIS	F	69	15	15	Port of Spain fish market, TRINIDAD	519
FALCIFORMIS	F	72	15	-	Dauphin Is., Alabama, U.S.A.	150
FALCIFORMIS	F	75	15	15	Port of Spain fish market, TRINIDAD	520
FALCIFORMIS	F	78	15	15	Port of Spain fish market, TRINIDAD	521
FALCIFORMIS	F	83	-	15	Port of Spain fish market, TRINIDAD	507
FALCIFORMIS	F	83	15	15	Port of Spain fish market, TRINIDAD	512
FALCIFORMIS	F	86	15	15	Port of Spain fish market, TRINIDAD	517
FALCIFORMIS	F	91	16	15	Port of Spain fish market, TRINIDAD	506
FALCIFORMIS	F	121	15	15	Port of Spain fish market, TRINIDAD	474
FALCIFORMIS	F	127	15	15	Port of Spain fish market, TRINIDAD	522
FALCIFORMIS	F	194	16	16	Moro Gulf, S. of Mindanao, PHILIPPINES	350
FALCIFORMIS	F	208	16	16	Moro Gulf, S. of Mindanao, PHILIPPINES	339

APPENDIX 1—(Continued)

Species	Sex	TL ^a	Ub	Lc	Locality	ID ^d
FALCIFORMIS	F	228	16	-	Moro Gulf, S. of Mindanao, PHILIPPINES	338
FALCIFORMIS	F	240	15	15	Moro Gulf, S. of Mindanao, PHILIPPINES	340
FALCIFORMIS	M	-	16	15	Moro Gulf, S. of Mindanao, PHILIPPINES	351
FALCIFORMIS	M	57	15	15	Moro Gulf, S. of Mindanao, PHILIPPINES	998
FALCIFORMIS	M	69	15	-	Port of Spain fish market, TRINIDAD	505
FALCIFORMIS	M	74	15	15	Port of Spain fish market, TRINIDAD	514
FALCIFORMIS	M	76	15	-	Port of Spain fish market, TRINIDAD	508
FALCIFORMIS	M	80	15	15	Port of Spain fish market, TRINIDAD	516
FALCIFORMIS	M	80	15	15	Port of Spain fish market, TRINIDAD	518
FALCIFORMIS	M	120	15	15	Port of Spain fish market, TRINIDAD	509
FALCIFORMIS	M	203	15	15	Moro Gulf, S. of Mindanao, PHILIPPINES	352
FALCIFORMIS	M	210	15	15	Moro Gulf, S. of Mindanao, PHILIPPINES	337
FALCIFORMIS	M	211	16	16	Moro Gulf, S. of Mindanao, PHILIPPINES	343
FALCIFORMIS	M	251	15	15	Port of Spain fish market, TRINIDAD	490
GALAPAGENSIS	?	-	14	-	J. L. B. Smith Inst. (no label), S. AFRICA	820
GALAPAGENSIS	?	-	14	14	Grand Commore, J. L. B. Smith Inst. (no number)	821
GALAPAGENSIS	?	-	13	13	Galapagos Islands (L.J.V.C. #0285), ECUADOR	836
GALAPAGENSIS	F	95	14	13	J. L. B. Smith Inst. (#006412), S. AFRICA	804
GALAPAGENSIS	F	106	14	14	Nihoa Island, (N.W. Hawaiian Islands), U.S.A.	544
GALAPAGENSIS	F	108	14	-	J. L. B. Smith Inst. (#006411), S. AFRICA	805
GALAPAGENSIS	F	114	13	14	J. L. B. Smith Inst. (#006420), S. AFRICA	807
GALAPAGENSIS	F	114	14	14	J. L. B. Smith Inst. (#006421), S. AFRICA	808
GALAPAGENSIS	F	119	13	-	J. L. B. Smith Inst. (#006422), S. AFRICA	810
GALAPAGENSIS	F	125	14	14	J. L. B. Smith Inst. (#006426), S. AFRICA	811
GALAPAGENSIS	F	132	14	14	J. L. B. Smith Inst. (#006424), S. AFRICA	814
GALAPAGENSIS	F	136	13	-	Socorro Is., Eastern Pacific, MEXICO	864
GALAPAGENSIS	F	138	14	13	J. L. B. Smith Inst. (#006423), S. AFRICA	816
GALAPAGENSIS	M	78	13	13	J. L. B. Smith Inst. (#006415), S. AFRICA	801
GALAPAGENSIS	M	95	14	-	J. L. B. Smith Inst. (#006416), S. AFRICA	802
GALAPAGENSIS	M	95	14	14	J. L. B. Smith Inst. (#006413), S. AFRICA	803
GALAPAGENSIS	M	111	14	14	J. L. B. Smith Inst. (#006419), S. AFRICA	806
GALAPAGENSIS	M	115	13	13	J. L. B. Smith Inst. (#006410), S. AFRICA	809
GALAPAGENSIS	M	127	14	13	J. L. B. Smith Inst. (#006414), S. AFRICA	812
GALAPAGENSIS	M	131	14	13	J. L. B. Smith Inst. (#006427), S. AFRICA	813
GALAPAGENSIS	M	137	14	14	J. L. B. Smith Inst. (#006425), S. AFRICA	815
GALAPAGENSIS	M	138	14	13	J. L. B. Smith Inst. (#006418), S. AFRICA	817
GALAPAGENSIS	M	142	14	13	Seaward side of Rabbit Island, Oahu, Hawaii, U.S.A.	572
GALAPAGENSIS	M	143	14	13	J. L. B. Smith Inst. (#006417), S. AFRICA	818
GALAPAGENSIS	M	148	-	13	J. L. B. Smith Inst. (#006428), S. AFRICA	819
ISODON	?	-	15	14	L.J.V.C. Collection	865
ISODON	F	121	15	14	Bulls Bay, nr. Charleston, S. Carolina, U.S.A.	399
ISODON	F	123	15	14	Bulls Bay, nr. Charleston, S. Carolina, U.S.A.	394
ISODON	F	126	14	15	Bulls Bay, nr. Charleston, S. Carolina, U.S.A.	395
ISODON	F	136	15	14	Bulls Bay, nr. Charleston, S. Carolina, U.S.A.	411
ISODON	F	137	14	-	29°20'N, 81°03'W (off Florida coast), U.S.A.	606
ISODON	F	146	15	14	29°17'N, 81°00'W (off Florida coast), U.S.A.	602
ISODON	F	146	15	14	29°17'N, 81°00'W (off Florida coast), U.S.A.	603
ISODON	F	151	15	14	29°20'N, 81°03'W (off Florida coast), U.S.A.	601
ISODON	F	151	15	15	29°17'N, 81°00'W (off Florida coast), U.S.A.	605
ISODON	F	154	15	14	29°17'N, 81°00'W (off Florida coast), U.S.A.	607
ISODON	F	156	15	14	29°17'N, 81°00'W (off Florida coast), U.S.A.	604
ISODON	M	107	15	14	Bulls Bay, nr. Charleston, S. Carolina, U.S.A.	410
ISODON	M	109	15	14	Bulls Bay, nr. Charleston, S. Carolina, U.S.A.	396
ISODON	M	116	15	14	Bulls Bay, nr. Charleston, S. Carolina, U.S.A.	397
ISODON	M	118	15	14	Bulls Bay, nr. Charleston, S. Carolina, U.S.A.	393
ISODON	M	119	15	14	Bulls Bay, nr. Charleston, S. Carolina, U.S.A.	409
ISODON	M	120	15	14	Bulls Bay, nr. Charleston, S. Carolina, U.S.A.	398
ISODON	M	124	14	14	Dauphin Is., Alabama, U.S.A.	138
ISODON	M	138	15	14	Bulls Bay, nr. Charleston, S. Carolina, U.S.A.	392

APPENDIX 1—(Continued)

Species	Sex	TL ^a	U ^b	L ^c	Locality	ID ^d
LEUCAS	?	-	13	12	J. L. B. Smith Inst. (no number assigned), S. AFRICA	763
LEUCAS	F	64	12	-	J. L. B. Smith Inst. (#006453), S. AFRICA	738
LEUCAS	F	68	12	12	J. L. B. Smith Inst. (#006463), S. AFRICA	739
LEUCAS	F	75	13	12	J. L. B. Smith Inst. (#006469), S. AFRICA	740
LEUCAS	F	121	13	12	J. L. B. Smith Inst. (#006448), S. AFRICA	745
LEUCAS	F	125	12	12	J. L. B. Smith Inst. (#006460), S. AFRICA	744
LEUCAS	F	134	13	12	J. L. B. Smith Inst. (#006435), S. AFRICA	746
LEUCAS	F	142	13	12	J. L. B. Smith Inst. (#006472), S. AFRICA	747
LEUCAS	F	167	12	12	J. L. B. Smith Inst. (#006443), S. AFRICA	749
LEUCAS	F	167	12	12	J. L. B. Smith Inst. (#006477), S. AFRICA	750
LEUCAS	F	168	13	12	Freetown (Sierra fisheries by catch), SIERRA LEONE	207
LEUCAS	F	174	13	12	J. L. B. Smith Inst. (#006476), S. AFRICA	751
LEUCAS	F	190	13	12	J. L. B. Smith Inst. (#006457), S. AFRICA	754
LEUCAS	F	202	13	12	J. L. B. Smith Inst. (#006466), S. AFRICA	755
LEUCAS	F	221	13	12	Off Cosgrove, Florida Keys, Florida, U.S.A.	562
LEUCAS	F	224	14	12	Ponce Inlet, Florida, U.S.A.	462
LEUCAS	F	227	12	12	J. L. B. Smith Inst. (#006445), S. AFRICA	758
LEUCAS	F	236	13	12	J. L. B. Smith Inst. (#006432), S. AFRICA	759
LEUCAS	F	249	13	12	J. L. B. Smith Inst. (#006470), S. AFRICA	760
LEUCAS	F	252	13	12	Freetown (Sierra fisheries by catch), SIERRA LEONE	210
LEUCAS	F	254	12	12	Ponce Inlet, Florida, U.S.A.	458
LEUCAS	F	257	12	-	Marathon, Florida Keys, Florida, U.S.A.	465
LEUCAS	F	260	13	13	Dauphin Is., Alabama, U.S.A.	255
LEUCAS	F	267	13	12	Dauphin Is., Alabama, U.S.A.	250
LEUCAS	F	284	12	12	J. L. B. Smith Inst. (#006430), S. AFRICA	762
LEUCAS	M	-	13	12	J. L. B. Smith Inst. (#006449), S. AFRICA	753
LEUCAS	M	78	13	12	J. L. B. Smith Inst. (#006461), S. AFRICA	741
LEUCAS	M	90	13	12	J. L. B. Smith Inst. (#006471), S. AFRICA	742
LEUCAS	M	116	13	12	J. L. B. Smith Inst. (#006452), S. AFRICA	743
LEUCAS	M	155	13	12	J. L. B. Smith Inst. (#006458), S. AFRICA	748
LEUCAS	M	184	13	12	J. L. B. Smith Inst. (#006446), S. AFRICA	752
LEUCAS	M	200	13	12	Marathon, Florida Keys, Florida, U.S.A.	472
LEUCAS	M	209	13	13	Sand shoal inlet, Eastern Shore, Virginia, U.S.A.	370
LEUCAS	M	211	13	12	J. L. B. Smith Inst. (#006437), S. AFRICA	756
LEUCAS	M	218	12	13	Smithsonian Field Station, Carribow Cay, BELIZE	171
LEUCAS	M	225	13	12	J. L. B. Smith Inst. (#006442), S. AFRICA	757
LEUCAS	M	231	12	-	Ponce Inlet, Florida, U.S.A.	451
LEUCAS	M	235	13	-	Acres Beach, Jacksonville, Florida, U.S.A.	53
LEUCAS	M	258	13	12	J. L. B. Smith Inst. (#006436), S. AFRICA	761
LIMBATUS	?	-	-	13	Freetown (Sierra fisheries by catch), SIERRA LEONE	227
LIMBATUS	?	-	15	13	Dauphin Is., Alabama, U.S.A.	6489
LIMBATUS	?	-	15	13	Dauphin Is., Alabama, U.S.A.	6490
LIMBATUS	?	-	15	14	Dauphin Is., Alabama, U.S.A.	6491
LIMBATUS	?	169	15	15	Ponce Inlet, Florida, U.S.A.	464
LIMBATUS	F	-	15	14	Jacksonville, Florida, U.S.A.	23
LIMBATUS	F	-	15	15	Ponce Inlet, Florida, U.S.A.	456
LIMBATUS	F	54	15	14	Turtle Islands, Sulu Sea (Navotas mkt.), PHILIPPINES	283
LIMBATUS	F	64	15	-	Turtle Islands, Sulu Sea (Navotas mkt.), PHILIPPINES	282
LIMBATUS	F	65	15	15	Turtle Islands, Sulu Sea (Navotas mkt.), PHILIPPINES	301
LIMBATUS	F	68	-	14	Freetown (Sierra fisheries by catch), SIERRA LEONE	226
LIMBATUS	F	73	15	14	Freetown (Sierra fisheries by catch), SIERRA LEONE	192
LIMBATUS	F	82	14	13	Freetown (Sierra fisheries by catch), SIERRA LEONE	196
LIMBATUS	F	85	15	14	Turtle Islands, Sulu Sea (Navotas mkt.), PHILIPPINES	302
LIMBATUS	F	87	15	15	Navotas mkt., Manila (from Palawan), PHILIPPINES	353
LIMBATUS	F	89	15	14	Freetown (Sierra fisheries by catch), SIERRA LEONE	197
LIMBATUS	F	92	15	13	Freetown (Sierra fisheries by catch), SIERRA LEONE	225
LIMBATUS	F	119	14	15	Bulls Bay, nr. Charleston, S. Carolina, U.S.A.	407
LIMBATUS	F	125	15	15	Bulls Bay, nr. Charleston, S. Carolina, U.S.A.	408
LIMBATUS	F	127	15	13	Dauphin Is., Alabama, U.S.A.	155

APPENDIX 1—(Continued)

Species	Sex	TL ^a	U ^b	L ^c	Locality	ID ^d
LIMBATUS	F	130	14	15	Bulls Bay, nr. Charleston, S. Carolina, U.S.A.	405
LIMBATUS	F	135	15	14	Dauphin Is., Alabama, U.S.A.	162
LIMBATUS	F	136	15	14	Bulls Bay, nr. Charleston, S. Carolina, U.S.A.	406
LIMBATUS	F	150	14	14	Freetown (Sierra fisheries by catch), SIERRA LEONE	187
LIMBATUS	F	167	15	14	Dauphin Is., Alabama, U.S.A.	161
LIMBATUS	M	65	15	15	Turtle Islands, Sulu Sea (Navotas mkt.), PHILIPPINES	280
LIMBATUS	M	66	15	-	Turtle Islands, Sulu Sea (Navotas mkt.), PHILIPPINES	281
LIMBATUS	M	88	14	14	Freetown (Sierra fisheries by catch), SIERRA LEONE	224
LIMBATUS	M	89	14	-	Freetown (Sierra fisheries by catch), SIERRA LEONE	222
LIMBATUS	M	91	15	14	Freetown (Sierra fisheries by catch), SIERRA LEONE	191
LIMBATUS	M	96	14	13	Dauphin Is., Alabama, U.S.A.	157
LIMBATUS	M	100	14	-	Freetown (Sierra fisheries by catch), SIERRA LEONE	204
LIMBATUS	M	106	15	13	Freetown (Sierra fisheries by catch), SIERRA LEONE	195
LIMBATUS	M	108	14	13	Dauphin Is., Alabama, U.S.A.	156
LIMBATUS	M	112	14	-	Dauphin Is., Alabama, U.S.A.	154
LIMBATUS	M	117	15	14	Dauphin Is., Alabama, U.S.A.	158
LIMBATUS	M	118	14	13	Dauphin Is., Alabama, U.S.A.	153
LIMBATUS	M	121	15	14	Dauphin Is., Alabama, U.S.A.	159
LIMBATUS	M	127	14	13	Dauphin Is., Alabama, U.S.A.	147
LIMBATUS	M	139	14	14	Freetown (Sierra fisheries by catch), SIERRA LEONE	211
LIMBATUS	M	148	-	13	Smithsonian Field Station, Caribbow Cay, BELIZE	170
LIMBATUS	M	154	15	14	Ponce Inlet, Florida, U.S.A.	453
LIMBATUS	M	155	14	14	Marathon, Florida Keys, Florida, U.S.A.	473
LIMBATUS	M	156	15	15	Ponce Inlet, Florida, U.S.A.	444
LIMBATUS	M	158	15	14	Ponce Inlet, Florida, U.S.A.	454
LIMBATUS	M	165	15	15	Ponce Inlet, Florida, U.S.A.	446
LIMBATUS	M	165	15	15	Marathon, Florida Keys, Florida, U.S.A.	468
LIMBATUS	M	176	15	15	Bulls Bay, nr. Charleston, S. Carolina, U.S.A.	377
LONGIMANUS	?	-	14	14	Grand Commore, J. L. B. Smith Inst. (no number)	787
LONGIMANUS	?	-	14	14	J. L. B. Smith Inst. (no number), S. AFRICA	788
LONGIMANUS	?	-	14	13	Grand Comore, J. L. B. Smith Inst. (no number)	789
LONGIMANUS	?	-	14	14	L.J.V.C. Collection (no locality data)	866
LONGIMANUS	F	124	13	-	03°18'N, 101°54'W nr. Shoyu Maru W. PACIFIC	837
LONGIMANUS	F	150	14	14	J. L. B. Smith Inst. (#006529), S. AFRICA	785
LONGIMANUS	F	159	14	-	J. L. B. Smith Inst. (#006527), S. AFRICA	786
LONGIMANUS	F	169	14	14	19°15'N, 160°49'W (200 m. SSW of Oahu, Hawaii) U.S.A.	541
LONGIMANUS	F	180	13	13	J. L. B. Smith Inst. (#006534), S. AFRICA	790
LONGIMANUS	F	211	14	14	J. L. B. Smith Inst. (#006525), S. AFRICA	791
LONGIMANUS	F	212	13	13	J. L. B. Smith Inst. (#006523), S. AFRICA	792
LONGIMANUS	F	214	13	13	J. L. B. Smith Inst. (#006530), S. AFRICA	793
LONGIMANUS	F	232	14	13	J. L. B. Smith Inst. (#006526), S. AFRICA	795
LONGIMANUS	F	232	16	13	J. L. B. Smith Inst. (#006521), S. AFRICA	796
LONGIMANUS	F	237	14	13	J. L. B. Smith Inst. (#006537), S. AFRICA	797
LONGIMANUS	F	238	14	13	J. L. B. Smith Inst. (#006522), S. AFRICA	798
LONGIMANUS	F	238	14	13	J. L. B. Smith Inst. (#006524), S. AFRICA	799
LONGIMANUS	F	250	13	13	J. L. B. Smith Inst. (#006533), S. AFRICA	800
LONGIMANUS	M	139	14	14	19°15'N, 160°49'W (200 m. SSW of Oahu, Hawaii) U.S.A.	543
LONGIMANUS	M	160	13	14	19°15'N, 160°49'W (200 m. SSW of Oahu, Hawaii) U.S.A.	542
LONGIMANUS	M	163	14	13	19°10'N, 160°51'W (off Hawaii), U.S.A.	610
LONGIMANUS	M	164	14	14	Nihoa, North West Hawaiian Islands, Hawaii, U.S.A.	609
LONGIMANUS	M	175	14	14	19°10'N, 160°51'W (off Hawaii), U.S.A.	611
LONGIMANUS	M	226	13	13	J. L. B. Smith Inst. (#006538), S. AFRICA	794
MELANOPTERUS	F	65	12	11	Anda, Pangasinan (Alaminos market), PHILIPPINES	263
MELANOPTERUS	F	65	11	11	Anda, Pangasinan (Alaminos market), PHILIPPINES	266
MELANOPTERUS	F	77	12	12	Anda, Pangasinan (Alaminos market), PHILIPPINES	261
MELANOPTERUS	M	65	12	12	Anda, Pangasinan (Alaminos market), PHILIPPINES	264
MELANOPTERUS	M	75	12	-	Anda, Pangasinan (Alaminos market), PHILIPPINES	262
MELANOPTERUS	M	75	12	11	Anda, Pangasinan (Alaminos market), PHILIPPINES	267
MELANOPTERUS	M	77	12	12	Anda, Pangasinan (Alaminos market), PHILIPPINES	265

APPENDIX 1—(Continued)

Species	Sex	TL ^a	U ^b	L ^c	Locality	ID ^d
MELANOPTERUS	M	86	12	11	Hundred Islands, Lingayen Gulf, PHILIPPINES	268
MELANOPTERUS	M	114	12	-	J. L. B. Smith Inst. (#006541), S. AFRICA	830
N. VELOX	?	69	13	10	Fish plant, Guyamas (L.J.V.C. # G-222), MEXICO	862
N. VELOX	?	73	13	11	Fish plant, Guyamas (L.J.V.C. # G-217), MEXICO	857
N. VELOX	?	106	13	12	Fish plant, Guyamas (L.J.V.C. # G-206), MEXICO	846
N. VELOX	?	106	13	10	Fish plant, Guyamas (L.J.V.C. # G-219), MEXICO	859
N. VELOX	?	110	13	10	Fish plant, Guyamas (L.J.V.C. # G-205), MEXICO	845
N. VELOX	?	110	12	12	Fish plant, Guyamas (L.J.V.C. # G-211), MEXICO	851
N. VELOX	?	110	13	11	Fish plant, Guyamas (L.J.V.C. # G-218), MEXICO	858
N. VELOX	?	113	14	-	Fish plant, Guyamas (L.J.V.C. # G-215), MEXICO	855
N. VELOX	?	115	12	12	Fish plant, Guyamas (L.J.V.C. # G-207), MEXICO	847
N. VELOX	?	117	13	10	Fish plant, Guyamas (L.J.V.C. # G-179), MEXICO	844
N. VELOX	?	119	13	11	Fish plant, Guyamas (L.J.V.C. # G-210), MEXICO	850
N. VELOX	?	119	13	12	Fish plant, Guyamas (L.J.V.C. # G-216), MEXICO	856
N. VELOX	?	124	13	10	Fish plant, Guyamas (L.J.V.C. # G-208), MEXICO	848
N. VELOX	?	124	12	10	Fish plant, Guyamas (L.J.V.C. # G-220), MEXICO	860
N. VELOX	?	124	12	10	Fish plant, Guyamas (L.J.V.C. # G-221), MEXICO	861
N. VELOX	?	125	13	11	Fish plant, Guyamas (L.J.V.C. # G-213), MEXICO	853
N. VELOX	?	128	-	10	Fish plant, Guyamas (L.J.V.C. # G-212), MEXICO	852
N. VELOX	?	128	13	10	Fish plant, Guyamas (L.J.V.C. # G-223), MEXICO	863
N. VELOX	?	132	13	11	Fish plant, Guyamas (L.J.V.C. # G-214), MEXICO	854
N. VELOX	?	135	12	10	Fish plant, Guyamas (L.J.V.C. # G-209), MEXICO	849
OBSCURUS	F	107	14	13	29°10'N, 80°48'W (off Florida coast), U.S.A.	596
OBSCURUS	F	112	14	13	29°10'N, 80°48'W (off Florida coast), U.S.A.	593
OBSCURUS	F	112	14	14	29°10'N, 80°48'W (off Florida coast), U.S.A.	594
OBSCURUS	F	113	14	14	29°10'N, 80°48'W (off Florida coast), U.S.A.	599
OBSCURUS	F	128	15	14	29°16'N, 80°25'W (off Florida coast), U.S.A.	591
OBSCURUS	F	181	14	14	29°06'N, 80°46'W (off Florida coast), U.S.A.	578
OBSCURUS	F	186	14	14	29°06'N, 80°45'W (off Florida coast), U.S.A.	588
OBSCURUS	F	227	14	14	29°16'N, 80°25'W (off Florida coast), U.S.A.	575
OBSCURUS	F	227	14	13	29°06'N, 80°46'W (off Florida coast), U.S.A.	576
OBSCURUS	F	255	15	14	Dauphin Is., Alabama, U.S.A.	94
OBSCURUS	F	261	15	14	Ocean City, Maryland, U.S.A.	246
OBSCURUS	F	269	14	14	Dauphin Is., Alabama, U.S.A.	95
OBSCURUS	F	270	15	14	29°02'N, 80°46'W (off Florida coast), U.S.A.	583
OBSCURUS	F	315	15	15	20 mi N. of Ponce Inlet, Florida, U.S.A.	587
OBSCURUS	M	105	14	13	29°06'N, 80°45'W (off Florida coast), U.S.A.	589
OBSCURUS	M	114	14	13	29°08'N, 80°57'W (off Florida coast), U.S.A.	595
OBSCURUS	M	170	14	-	29°16'N, 80°25'W (off Florida coast), U.S.A.	592
OBSCURUS	M	174	14	13	29°10'N, 80°48'W (off Florida coast), U.S.A.	580
OBSCURUS	M	175	14	13	29°10'N, 80°48'W (off Florida coast), U.S.A.	579
OBSCURUS	M	178	15	14	29°16'N, 80°25'W (off Florida coast), U.S.A.	582
OBSCURUS	M	182	15	14	29°09'N, 80°47'W (off Florida coast), U.S.A.	584
OBSCURUS	M	183	14	14	29°06'N, 80°45'W (off Florida coast), U.S.A.	577
OBSCURUS	M	202	14	14	29°07'N, 80°46'W (off Florida coast), U.S.A.	586
OBSCURUS	M	205	15	14	29°07'N, 80°46'W (off Florida coast), U.S.A.	581
OBSCURUS	M	230	15	15	29°10'N, 80°47'W (off Florida coast), U.S.A.	585
PEREZI	?	-	13	-	Blau blau, Curacao (L.J.V.C. #0251), CURACAO	838
PEREZI	F	129	13	12	Deep Water Caye, Grand Bahama Is., BAHAMAS	235
PEREZI	F	186	13	11	Marathon, Florida Keys, Florida, U.S.A.	471
PEREZI	F	207	13	12	Curlew Cay nr. Carribow Cay, Dangriga, BELIZE	176
PEREZI	M	77	13	11	Smithsonian Field Station, Carribow Cay, BELIZE	172
PEREZI	M	100	13	11	Smithsonian Field Station, Carribow Cay, BELIZE	165
PEREZI	M	132	13	12	Deep Water Caye, Grand Bahama Is., BAHAMAS	233
PEREZI	M	137	13	12	Smithsonian Field Station, Carribow Cay, BELIZE	166
PEREZI	M	154	13	12	Glover's Reef, Dangriga, BELIZE	179
PEREZI	M	171	13	12	Smithsonian Field Station, Carribow Cay, BELIZE	174
PEREZI	M	173	13	12	Smithsonian Field Station, Carribow Cay, BELIZE	169
PLUMBEUS	?	-	14	14	Off Cogrove, Florida Keys, Florida, U.S.A.	564

APPENDIX 1—(Continued)

Species	Sex	TL ^a	U ^b	L ^c	Locality	ID ^d
PLUMBEUS	F	-	14	14	14 Bayshore, Long Island, New York, U.S.A.	425
PLUMBEUS	F	74	-	13	Magothy Bay, Southern Virginia, U.S.A.	365
PLUMBEUS	F	90	-	13	Sand shoal inlet, Eastern Shore, Virginia, U.S.A.	369
PLUMBEUS	F	149	14	14	Makapu Point, Oahu, Hawaii, U.S.A.	556
PLUMBEUS	F	164	14	13	Ponce Inlet, Florida, U.S.A.	455
PLUMBEUS	F	167	14	14	Maunalua Bay, S. Oahu, Hawaii, U.S.A.	570
PLUMBEUS	F	176	14	14	Point Pleasant, New Jersey, U.S.A.	415
PLUMBEUS	F	176	-	13	Maunalua Bay, S. Oahu, Hawaii, U.S.A.	571
PLUMBEUS	F	178	14	14	Bayshore, Long Island, New York, U.S.A.	418
PLUMBEUS	F	180	14	14	Bayshore, Long Island, New York, U.S.A.	417
PLUMBEUS	F	180	14	14	Makapu Point, Oahu, Hawaii, U.S.A.	555
PLUMBEUS	F	182	14	14	Point Pleasant, New Jersey, U.S.A.	414
PLUMBEUS	F	185	14	14	Ocean City, Maryland, U.S.A.	236
PLUMBEUS	F	185	14	13	Bayshore, Long Island, New York, U.S.A.	426
PLUMBEUS	F	194	15	14	Ponce Inlet, Florida, U.S.A.	463
PLUMBEUS	F	198	14	13	Sand shoal inlet, Eastern Shore, Virginia, U.S.A.	371
PLUMBEUS	F	200	14	14	Bayshore, Long Island, New York, U.S.A.	419
PLUMBEUS	F	202	14	14	Magothy Bay, Southern Virginia, U.S.A.	363
PLUMBEUS	F	202	14	14	Bayshore, Long Island, New York, U.S.A.	421
PLUMBEUS	F	202	14	13	Off Cosgrove, Florida Keys, Florida, U.S.A.	557
PLUMBEUS	F	204	14	14	Magothy Bay, Southern Virginia, U.S.A.	362
PLUMBEUS	F	207	14	13	Ponce Inlet, Florida, U.S.A.	449
PLUMBEUS	F	210	14	14	Bayshore, Long Island, New York, U.S.A.	428
PLUMBEUS	F	211	14	-	Jacksonville, Florida, U.S.A.	41
PLUMBEUS	F	212	14	14	Off Cosgrove Cosgrove, Florida Keys, Florida, U.S.A.	559
PLUMBEUS	F	213	14	13	Ocean City, Maryland, U.S.A.	242
PLUMBEUS	M	84	14	14	Samar, Visayan Sea (Cebu City mkt.), PHILIPPINES	323
PLUMBEUS	M	131	-	14	Bulls Bay, nr. Charleston, S. Carolina, U.S.A.	378
PLUMBEUS	M	170	14	13	Bayshore, Long Island, New York, U.S.A.	424
PLUMBEUS	M	173	-	14	Ponce Inlet, Florida, U.S.A.	447
PLUMBEUS	M	177	-	15	Ocean City, Maryland, U.S.A.	247
PLUMBEUS	M	180	14	14	Bayshore, Long Island, New York, U.S.A.	423
PLUMBEUS	M	198	14	14	Ponce Inlet, Florida, U.S.A.	448
POROSUS	?	-	14	12	Fish plant, Guyamas (L.J.V.C. # G-98), MEXICO	842
POROSUS	?	-	13	12	Fish plant, Guyamas (L.J.V.C. # G-226), MEXICO	843
POROSUS	F	54	-	13	Port of Spain fish market, TRINIDAD	480
POROSUS	F	55	13	13	Port of Spain fish market, TRINIDAD	483
POROSUS	F	55	13	13	Port of Spain fish market, TRINIDAD	484
POROSUS	F	81	13	-	Port of Spain fish market, TRINIDAD	531
POROSUS	F	83	14	13	Port of Spain fish market, TRINIDAD	530
POROSUS	F	91	13	14	Port of Spain fish market, TRINIDAD	529
POROSUS	F	102	13	13	Port of Spain fish market, TRINIDAD	533
POROSUS	F	106	13	13	Port of Spain fish market, TRINIDAD	532
POROSUS	F	106	13	13	Port of Spain fish market, TRINIDAD	534
POROSUS	M	54	-	13	Port of Spain fish market, TRINIDAD	536
POROSUS	M	56	-	13	Port of Spain fish market, TRINIDAD	479
POROSUS	M	56	13	13	Port of Spain fish market, TRINIDAD	537
POROSUS	M	57	13	12	Port of Spain fish market, TRINIDAD	478
POROSUS	M	61	13	13	Port of Spain fish market, TRINIDAD	523
POROSUS	M	72	13	-	Port of Spain fish market, TRINIDAD	528
POROSUS	M	73	13	13	Port of Spain fish market, TRINIDAD	525
POROSUS	M	74	13	13	Port of Spain fish market, TRINIDAD	526
POROSUS	M	76	13	13	Port of Spain fish market, TRINIDAD	527
POROSUS	M	84	13	13	Port of Spain fish market, TRINIDAD	524
POROSUS	M	86	13	13	Port of Spain fish market, TRINIDAD	475
POROSUS	M	99	13	13	Port of Spain fish market, TRINIDAD	476
POROSUS	M	99	13	13	Port of Spain fish market, TRINIDAD	477
SEALEI	F	49	12	-	Turtle Islands, Sulu Sea (Navotas mkt.), PHILIPPINES	279
SEALEI	F	54	12	11	Turtle Islands, Sulu Sea (Navotas mkt.), PHILIPPINES	305

APPENDIX 1—(Continued)

Species	Sex	TL ^a	U ^b	L ^c	Locality	ID ^d
SEALEI	F	67	13	12	Turtle Islands, Sulu Sea (Navotas mkt.), PHILIPPINES	304
SEALEI	F	69	12	12	Turtle Islands, Sulu Sea (Navotas mkt.), PHILIPPINES	276
SEALEI	F	80	12	13	Southern Palawan (Navotas mkt.), PHILIPPINES	295
SEALEI	F	83	13	13	Turtle Islands, Sulu Sea (Navotas mkt.), PHILIPPINES	303
SEALEI	F	84	12	12	Turtle Islands, Sulu Sea (Navotas mkt.), PHILIPPINES	273
SEALEI	F	84	13	12	Turtle Islands, Sulu Sea (Navotas mkt.), PHILIPPINES	310
SEALEI	F	85	12	12	Turtle Islands, Sulu Sea (Navotas mkt.), PHILIPPINES	274
SEALEI	F	85	13	13	Turtle Islands, (Navotas Fish Market), PHILIPPINES	302
SEALEI	M	56	-	11	Turtle Islands, Sulu Sea (Navotas mkt.), PHILIPPINES	307
SEALEI	M	59	12	11	Turtle Islands, Sulu Sea (Navotas mkt.), PHILIPPINES	306
SEALEI	M	61	12	12	Turtle Islands, Sulu Sea (Navotas mkt.), PHILIPPINES	278
SEALEI	M	63	13	12	Turtle Islands, Sulu Sea (Navotas mkt.), PHILIPPINES	277
SEALEI	M	73	-	12	Turtle Islands, Sulu Sea (Navotas mkt.), PHILIPPINES	275
SEALEI	M	76	12	12	Southern Palawan (Navotas mkt.), PHILIPPINES	292
SEALEI	M	77	12	12	Southern Palawan (Navotas mkt.), PHILIPPINES	290
SEALEI	M	77	12	12	Southern Palawan (Navotas mkt.), PHILIPPINES	293
SEALEI	M	78	-	11	Southern Palawan (Navotas mkt.), PHILIPPINES	291
SEALEI	M	78	13	12	Southern Palawan (Navotas mkt.), PHILIPPINES	294
SEALEI	M	81	-	11	Turtle Islands, Sulu Sea (Navotas mkt.), PHILIPPINES	299
SORRAH	?	86	-	12	Navotas Fish Landing, Manila, PHILIPPINES	259
SORRAH	F	52	12	12	Navotas mkt., Manila (from Palawan), PHILIPPINES	360
SORRAH	F	55	12	12	Navotas mkt., Manila (from Palawan), PHILIPPINES	359
SORRAH	F	55	12	-	Navotas mkt., Manila (from Palawan), PHILIPPINES	361
SORRAH	F	56	12	11	Navotas mkt., Manila (from Palawan), PHILIPPINES	358
SORRAH	F	86	-	11	Turtle Islands, Sulu Sea (Navotas mkt.), PHILIPPINES	300
SORRAH	F	88	13	12	S.China Sea nr. Palawan (Navotas mkt.), PHILIPPINES	296
SORRAH	M	89	12	13	S.China Sea nr. Palawan (Navotas mkt.), PHILIPPINES	297
WHEELERI	?	-	13	13	J. L. B. Smith Inst. (no number)	828
WHEELERI	?	124	13	12	J. L. B. Smith Inst. (#006407), MAURITIUS	829
WHEELERI	F	123	13	13	J. L. B. Smith Inst. (#006408)	827
WHEELERI	M	137	13	13	South side of Tiran Is. at "Melba," EGYPT	8
WHEELERI	M	159	13	12	J. L. B. Smith Inst. (#006409)	826

^a Total length, cm, of shark from which jaw was taken.^b Number of teeth present in right half of upper jaw.^c Number of teeth present in right half of lower jaw.^d Assigned field number (in computer data base).

APPENDIX 2

SAS Routines for Procedures Used

ROUTINE I

This program filled in missing measurements by averaging measurements from teeth on each side if present. Run before the "rothing" procedure (Routine II) to minimize loss of data brought about by interpolation. This is an example for the subset of the *falciformis* species data. Logic annotated with comments in italics in the form of /* comment */.

```

data new; set data.gavin; if species="FALCIFOR";
PROC SORT DATA=NEW; by species id jaw toothpos;
/* The following arrays are used—all of the measurements and centroid size. Two lag arrays are used in order to have three teeth measurements available—one each side of the one with missing values.*/
DATA new2; SET new; by species id jaw;
ARRAY DIST{28} DIS_AB-numeric-CSIZE;
ARRAY L1DIST{28} LONE1-LONE28;
ARRAY L2DIST{28} LTWO1-LTWO28;
ARRAY NDIST{28} NDIS1-NDIS28;
/* creates the lagged variables */
ljaw=lag1(jaw);
lid=lag1(id);
llastpos=lag1(lastpos);
llastpo=lag2(lastpos);
ltlthpos=lag1(toothpos);
lltthpos=lag2(toothpos);
lpositio=lag1(position);
DO I=1 TO 28;
  L1DIST{I}=LAG1(DIST{I});
  L2DIST{I}=LAG2(DIST{I});
  if L1DIST{I}= . THEN L1DIST{I}=0;
  if L2DIST{I}= . then L2DIST{I}=0;
  if DIST{I}= . then DIST{I}=0;
END;
if first.jaw then ncnt=0;
DO I=1 to 28;
  ndist{i}=l1dist{i};
  if lastpos = llastpo then do;
    /* takes average of values on either side if missing */
    IF L1DIST{i}= 0 and DIST{i} ne 0 and L2DIST{i}
      ne 0
      then ndist{i}= (dist{i}+l2dist{i})/2;
  end;
END;
if first.jaw = 0 then do; toothpos=ltlthpos;
  do i=1 to 28; if ndist{i}=0 then ndist{i}=.; end;
  output; end;
if last.jaw then do;
  do i=1 to 28;
    ndist{i}=dist{i};
    if ndist{i}=0 then ndist{i}=.; end;
    lpositio=position;
    ltlthpos=lastpos;
    output; end;
drop i lone1-lone28 ltwo1-ltwo28 dis_ab-numeric-csize
ncnt llastpos llastpo toothpos ljw lid lltlthpos position;
data data.falci; set new2;
ARRAY OLD{28} ndis1-numeric-ndis28;
array new{28}

```

```

DIS_AB DIS_AJ DIS_AM DIS_BC DIS_BI DIS_BL
DIS_CD DIS_CL DIS_CM
DIS_DE DIS_DL DIS_EF DIS_EL DIS_EM DIS_FG
DIS_FI DIS_FL DIS_GH
DIS_GM DIS_HI DIS_IJ DIS_IM DIS_KL DIS_LM
DIS_CE DIS_BJ DIS_FH
CSIZE;
do i=1 to 28;
new{i}=old{i};
end;
position=lpositio;
toothpos=ltlthpos;
drop ltlthpos ndis1-numeric-ndis28;
/* proc print data=new; */
run;

```

ROUTINE II

This program is used to interpolate measurements within a tooth series. The procedure is referred to as "Rething" after Louise Roth who first suggested it. The program yields jaws containing 10 "homologized" pseudoteeth in a series. The procedure uses the lag feature of SAS. Logic annotated using /* comment */ of SAS. Note all data.fn type entries refer to disk data sets, usually put on a scratch disk, from tape because of their large size.

```

data data.gavsub; /* new data set after reduction to 10 teeth */
set data.gavred; /* data set with all teeth available */
idjaw=id||jaw; /* idjaw—variable to uniquely define each jaw for each specimen */
/* SORT below arranges obs. by tooth position, within jaw, within specimen */
PROC SORT DATA=DATA.GAVSUB; BY IDJAW
TOOTHPOS;
/* creates a data set with number of teeth in each jaw = LASTTOOTH */
DATA DATA.GCOUNT; SET DATA.GAVSUB; BY
IDJAW TOOTHPOS;
LASTTOOTH=TOOTHPOS;
IF LAST.IDJAW THEN OUTPUT;
/* if last tooth in jaw creates 1 record per jaw */
KEEP IDJAW LASTTOOTH;
/* next step puts the count of number of teeth in each tooth record */
DATA lastpos; MERGE DATA.GAVSUB
DATA.GCOUNT; BY IDJAW;
IDNO = _N_;
/* NOW BEGINS THE HEART OF THE PROGRAM THAT DOES THE "ROTHING"
four arrays required—with variables for each of the 28 measurements: DIST—the array of input data
L1DIST—the array of lagged data, lagged by 1 tooth
L2DIST—the array of lagged data, lagged by 2 teeth
NDIST—the new interpolated data */
DATA GAVCONV; SET LASTPOS; BY IDJAW;
ARRAY DIST
  DIS_AB DIS_AJ DIS_AM DIS_BC DIS_BI DIS_BL
  DIS_CD DIS_CL DIS_CM

```

```

DIS_DE DIS_DL DIS_EF DIS_EL DIS_EM DIS_FG
DIS_FI DIS_FL DIS_GH
DIS_GM DIS_HI DIS_IJ DIS_IM DIS_KL DIS_LM
DIS_CE DIS_BJ DIS_FH CSIZE;
ARRAY L1DIST
L1S_AB L1S_AJ L1S_AM L1S_BC L1S_BI L1S_BL
L1S_CD L1S_CL L1S_CM
L1S_DE L1S_DL L1S_EF L1S_EL L1S_EM L1S_FG
L1S_FI L1S_FL L1S_GH
L1S_GM L1S_HI L1S_IJ L1S_IM L1S_KL L1S_LM
L1S_CE L1S_BJ L1S_FH L1SIZE;
ARRAY L2DIST
L2S_AB L2S_AJ L2S_AM L2S_BC L2S_BI L2S_BL
L2S_CD L2S_CL L2S_CM
L2S_DE L2S_DL L2S_EF L2S_EL L2S_EM L2S_FG +
L2S_FI L2S_FL L2S_GH L2S_GM L2S_HI L2S_IJ
L2S_IM L2S_KL L2S_LM L2S_CE L2S_BJ L2S_FH
L2SIZE;
ARRAY NDIST
NIS_AB NIS_AJ NIS_AM NIS_BC NIS_BI NIS_BL
NIS_CD NIS_CL NIS_CM
NIS_DE NIS_DL NIS_EF NIS_EL NIS_EM NIS_FG
NIS_FI NIS_FL NIS_GH
NIS_GM NIS_HI NIS_IJ NIS_IM NIS_KL NIS_LM
NIS_CE NIS_BJ NIS_FH NSIZE;
/* the loop below operates over all variables and creates
the lags */
DO OVER DIST;
L1DIST=LAG1(DIST);
L2DIST=LAG2(DIST);
if L1DIST=. THEN L1DIST=0;
if L2DIST=. THEN L2DIST=0;
END;
TOTPCT=ROUND((LASTooth/10),.1);
/* initialize each new jaw to be 0 */
IF FIRST.IDJAW THEN DO;
DO OVER DIST;
PCT1=1.0; PCT2=0.0; PCT3=0.0;
LPCT1=1.0; LPCT2=0.0;
RETAIN PCT1-PCT3 LPCT1-LPCT2;
RETURN;
END;
/* since we know the first record will never be output, this
section
applies to all records but the first */
IF FIRST.IDJAW NE 1 THEN DO;
IF NEED3=1 THEN DO;
/* executes in cases where need to go to a 3rd record to
complete */
PCT3=PCT2;
PCT2=PCT1;
PCT1=(TOTPCT-(PCT2+PCT3));
LPCT2=0;
LPCT1=1-PCT1;
NEED3=0;
END;
ELSE DO;
/* executes on second record and determines if a third is
needed */
PCT2=LPCT1; /* assigns last tooth the value left
over */
PCT1=TOTPCT-PCT2;
LPCT1=1-PCT1;
IF PCT1 GT 1 THEN DO;
PCT1=1;
LPCT1=0; /* sets back to 0 */
IF PCT2 GT 0 THEN DO;
NEED3=1; /* if true, need a 3rd record */
RETAIN NEED3;
END;
RETURN; /* sends it back to get another record */
END;
END;
PCTALLOC=PCT1+PCT2+PCT3;
/* when we have the right pcts, execute & output */
IF (PCT1+PCT2+PCT3)=TOTPCT THEN DO;
DO OVER DIST;
NDIST=(PCT1*DIST
PCT2*L1DIST+PCT3*L2DIST)/TOTPCT;
if pct3>0 and pct3*I2dist=0 then ndist=.;
if pct2>0 and pct2*I1dist=0 then ndist=.;
END;
OUTPUT;
PCT3=0; /* if pct3 has a value, need to set it back to
0 */
END;
/* This checks to see that the program is working. Will
write out final data set with POSITIONS set to letters.
*/
DATA DATA.GAV10;
SET GAVconv; by idjaw;
if first.idjaw then newpos=1;
if first.idjaw = 0 then newpos +1;
if newpos=1 then POSITION="A";
if newpos=2 then POSITION="B";
if newpos=3 then POSITION="C";
if newpos=4 then POSITION="D";
if newpos=5 then POSITION="E";
if newpos=6 then POSITION="F";
if newpos=7 then POSITION="G";
if newpos=8 then POSITION="H";
if newpos=9 then POSITION="I";
if newpos=10 then POSITION="J";
KEEP SPECIES SEX TOTALL MATURITY ID JAW
TOOTHPOS NEWPOS POSITION
LASTOOTH FLAG1 FLAG2
NIS_AB NIS_AJ NIS_AM NIS_BC NIS_BI NIS_BL
NIS_CD NIS_CL NIS_CM
NIS_DE NIS_DL NIS_EF NIS_EL NIS_EM NIS_FG
NIS_FI NIS_FL NIS_GH NIS_GM NIS_HI NIS_IJ
NIS_IM NIS_KL NIS_LM NIS_CE NIS_BJ NIS_FH
NSIZE;
RUN;

ROUTINE III
This program divides the data set into a training
or "LEARN" data set and a "TEST" data set,
based on random assignment (uppers, positions E
and F only). Includes reidentification of original
LEARN data, cross-validation of learn data set—
using leave one out method, and a more realistic
test using the "TEST" data. Though it was run as
a separate program, we have added the program
that does the canonical variates on to the end since
the first part is the same up to the point indicated.

```

```

data upper; set data.gav10n2; /* 10 toothed rothed data
set */
if jaw='U';
if position='E' or position='F'; /* uses 'best' postions E
and F */
array any
NIS_BC NIS_CD NIS_DE NIS_EF NIS_FI NIS_BI
NIS_CE NIS_CL NIS_EL
NIS_BL NIS_FL NIS_KL NIS_LM NIS_IM NIS_AM
NIS_GM;
do over any; /* divide through by centroid size */
  ANY=ANY/nsize;
if any ne .;
end;
proc sort data=upper; by id;
data rndord; set upper; by id; /* assigns random nos. to
all sharks */
seed=974153821;
if first.id=1 then do;
  rndno=ranuni(seed);
  output;
end;
keep species id rndno;
proc sort data=rndord; by species rndno;
data new; set rndord; by species;
/* NEW contains only 1st 8 random shark ID's */
if first.species=1 then i=0;
i+1;
if i<9;
proc sort data=new; by id;
data new1; merge upper new; by id;
data learn; set new1;
if rndno<>; /* LEARN contains randomly selected in-
dividuals */
proc freq data=learn; table species;
/* to check that counts are 8 or less */
data test; set new1; /* TEST contains the rest of the
individuals */
if rndno=.;
proc freq data=test; table species; /* count of test data
set */
/* I. STEPS BELOW produce data for figs. 11a, 11b,
and 11c */
proc discrim data=learn testdata=test pool=yes cross-
validate;
class species;
var NIS_BC NIS_CD NIS_DE NIS_EF NIS_FI NIS_BI
NIS_CE NIS_CL NIS_EL
NIS_BL NIS_FL NIS_KL NIS_LM NIS_IM NIS_AM
NIS_GM;
run;
/* II. STEPS BELOW produce data for figs. 12 and 13.
*/
proc discrim ncan=16 distance data=learn pool=yes
out=canout
outstat=canmns;
class species;
var NIS_BC NIS_CD NIS_DE NIS_EF NIS_FI NIS_BI
NIS_CE NIS_CL NIS_EL
NIS_BL NIS_FL NIS_KL NIS_LM NIS_IM NIS_AM
NIS_GM;
data mnsout; set canmns;
if _TYPE_="CANMEAN";
keep species NIS_BC;
/* it turns out the canonical means are repeated for each

```

variable— so keeping the first one here retains just one set of the canonical means */
proc sort data=mnsout; by species;
data; set mnsout;
/* this allows preparation of a file for plotting in other
programs on a MAC or PC */
FILE 'CANMNS ASC' lrecl=100;
PUT SPECIES ; dr 1-8 NIS_BC;
RUN;

ROUTINE IV

This program carries out a Discriminant Function Analysis on a data set based on upper tooth positions E and F. Since the space is high dimensional we pick specific species (see below) to examine in the two-dimensional projection that best exposes their cluster separation.

```

title 'Best View of triplets /8 spec.rndm, pos E&F=learn,
10N2';
data upper; set data.gav10n2;
if jaw='U';
if position='E' or position='F';
array any
NIS_BC NIS_CD NIS_DE NIS_EF NIS_FI NIS_BI
NIS_CE NIS_CL NIS_EL
NIS_BL NIS_FL NIS_KL NIS_LM NIS_IM NIS_AM
NIS_GM;
do over any;
  ANY=ANY/nsize; /* this corrects to centroid size */
if any ne .;
end;
proc sort data=upper; by id; /* sort by specimen—only
uppers */
data rndord; set upper; by id;
seed=974153821; /* next few steps add randnumber to
record */
if first.id=1 then do;
  rndno=ranuni(seed);
  output;
end;
keep species id rndno;
/* the sort puts the specimens in random order within
each species */
proc sort data=rndord; by species rndno;
/* the next 4 steps selects the first 8 specimens (16 teeth)
and puts into a new file called new */
data new; set rndord; by species;
if first.species=1 then i=0;
i+1;
if i<9;
proc sort data=new; by id;
/* the following merge— creates missing values for rndno
for specimens not selected in the previous stage */
data new1; merge upper new; by id;
/* the learn data set is the one then which has the rndno
<>. */
data learn; set new1;
if rndno<>:;
/* we now get a count of the number of teeth for each
species */
proc freq data=learn; table species;
/* A discriminant function is run with canonical variates
using the learn data set and pooling within covariance
matrices.
```

The canonical variates are written to a file called mns.

```

*/,
proc discrim outstat=mns canonical out=canscrs
data=learn pool=yes;
class species;
var NIS_BC NIS_CD NIS_DE NIS_EF NIS_FI NIS_BI
NIS_CE NIS_CL NIS_EL
NIS_BL NIS_FL NIS_KL NIS_LM NIS_IM NIS_AM
NIS_GM;
data mnsout; set mns; /* contains only the canonical
means */
if _TYPE_="CANMEAN";
keep species NIS_BC;
proc sort data=mnsout; by species;
data cnsout; set canscrs; /* contains the canonical variate
scores */
keep species can1-can16;
proc sort data=cnsout; by species;
*proc print data=mnsout;
*proc print data=cnsout;
*proc gplot data=cnsout; *plot can2*can1=species;
/* need to go into matrix routine (IML) to extract data
for species of interest and perform functions as indicated */
proc iml;
use mnsout;
read all into X(|rowname=species|); /* canonical means
*/
canspecs=species;
z=shape(X,22); /* z has size 16×22—for 22 species */
print z;
use cnsout;
read all into Y(|rowname=species|);
/* select species triplet—5th, 11th, and 13th species in
this example run */
ind={5 11 13};
ztrip=z(|ind,|); /* z now reduced to scores for 3 species
only */
spesel=canspecs(|ind,|); /* also species list */
print ind spesel;
/* print ztrip; */
call svd(v,d,u,ztrip);
/* does a singular value decomposition of the data- which
is equivalent to principal components of the scores for the
3 species */
u=u(|,1:3|); /* keep only 3 eigenvectors */
print u;
w=y*u; /* PC scores for three species */
/* print w; */
create wout from w[rownames=species]; /* write to ex-
ternal file */
append from w[rownames=species];
/* proc print data=wout; */
*proc gplot; *plot col2*col1=species; /* best 2-d projec-
tion */
run;
DATA; SET Wout;
FILE 'triple ASC' lrecl=100;
/* creates an ascii file of scores for further manipulation
in external program */
PUT
SPECIES ; dr
col1
col2

```

col3 ;
run;

ROUTINE V

This program is the basis for several figures in the text. The training data set data comprises "homologized" jaws, containing 10 pseudoteeth (A–J) with the naming conventions:

LORIG—for original data lower; LMIR—for mirror image lower (the opposite side); UORIG—for original data upper; UMIR—for mirror image upper. Each shark used in the training data set has 40 teeth (10 "homologized" teeth per tooth series × 4 jaw quadrants). The training data set contains 8 sharks selected at random from each species. The test data comprise all teeth in the original data set not used in the training data set. These test data are not subjected to the "homologizing" procedure that reduces the number of teeth in a series to 10, but rather comprise the original teeth measured. Accordingly, the test data consist of jaws with differing numbers of teeth (up to 16).

DATA NEW; SET DATA.GAV10X2;
/* NEW contains all of the tooth positions in all 4 quad-
rants */
IF JAW='L' AND SIDE='ORIG' AND POSI-
TION='A' THEN GRP='LORIGA';
IF JAW='L' AND SIDE='ORIG' AND POSITION='B'
THEN GRP='LORIGB';
IF JAW='L' AND SIDE='ORIG' AND POSITION='C'
THEN GRP='LORIGC';
IF JAW='L' AND SIDE='ORIG' AND POSITION='D'
THEN GRP='LORIGD';
IF JAW='L' AND SIDE='ORIG' AND POSITION='E'
THEN GRP='LORIGE';
IF JAW='L' AND SIDE='ORIG' AND POSITION='F'
THEN GRP='LORIGF';
IF JAW='L' AND SIDE='ORIG' AND POSI-
TION='G' THEN GRP='LORIGG';
IF JAW='L' AND SIDE='ORIG' AND POSITION='H'
THEN GRP='LORIGH';
IF JAW='L' AND SIDE='ORIG' AND POSITION='I'
THEN GRP='LORIGI';
IF JAW='L' AND SIDE='ORIG' AND POSITION='J'
THEN GRP='LORIGJ';
IF JAW='L' AND SIDE='MIR' AND POSITION='A'
THEN GRP='LMIR'A';
IF JAW='L' AND SIDE='MIR' AND POSITION='B'
THEN GRP='LMIRB';
IF JAW='L' AND SIDE='MIR' AND POSITION='C'
THEN GRP='LMIRC';
IF JAW='L' AND SIDE='MIR' AND POSITION='D'
THEN GRP='LMIRD';
IF JAW='L' AND SIDE='MIR' AND POSITION='E'
THEN GRP='LMIRE';
IF JAW='L' AND SIDE='MIR' AND POSITION='F'
THEN GRP='LMIRF';
IF JAW='L' AND SIDE='MIR' AND POSITION='G'
THEN GRP='LMIRG';
IF JAW='L' AND SIDE='MIR' AND POSITION='H'
THEN GRP='LMIRH';

```

IF JAW='L' AND SIDE='MIR' AND POSITION='I'
THEN GRP='LMIRI';
IF JAW='L' AND SIDE='MIR' AND POSITION='J'
THEN GRP='LMIRJ';
IF JAW='U' AND SIDE='ORIG' AND POSITION='A' THEN GRP='UORIGA';
IF JAW='U' AND SIDE='ORIG' AND POSITION='B' THEN GRP='UORIGB';
IF JAW='U' AND SIDE='ORIG' AND POSITION='C' THEN GRP='UORIGC';
IF JAW='U' AND SIDE='ORIG' AND POSITION='D' THEN GRP='UORIGD';
IF JAW='U' AND SIDE='ORIG' AND POSITION='E' THEN GRP='UORIGE';
IF JAW='U' AND SIDE='ORIG' AND POSITION='F' THEN GRP='UORIGF';
IF JAW='U' AND SIDE='ORIG' AND POSITION='G' THEN GRP='UORIGG';
IF JAW='U' AND SIDE='ORIG' AND POSITION='H' THEN GRP='UORIGH';
IF JAW='U' AND SIDE='ORIG' AND POSITION='I' THEN GRP='UORIGI';
IF JAW='U' AND SIDE='ORIG' AND POSITION='J' THEN GRP='UORIGJ';
IF JAW='U' AND SIDE='MIR' AND POSITION='A' THEN GRP='UMIRA';
IF JAW='U' AND SIDE='MIR' AND POSITION='B' THEN GRP='UMIRB';
IF JAW='U' AND SIDE='MIR' AND POSITION='C' THEN GRP='UMIRC';
IF JAW='U' AND SIDE='MIR' AND POSITION='D' THEN GRP='UMIRD';
IF JAW='U' AND SIDE='MIR' AND POSITION='E' THEN GRP='UMIRE';
IF JAW='U' AND SIDE='MIR' AND POSITION='F' THEN GRP='UMIRF';
IF JAW='U' AND SIDE='MIR' AND POSITION='G' THEN GRP='UMIRG';
IF JAW='U' AND SIDE='MIR' AND POSITION='H' THEN GRP='UMIRH';
IF JAW='U' AND SIDE='MIR' AND POSITION='I' THEN GRP='UMIRI';
IF JAW='U' AND SIDE='MIR' AND POSITION='J' THEN GRP='UMIRJ';
proc sort data= NEW; by id; /* this sorts the specimens by shark ID
RNDORD contains the IDs of the randomly selected sharks */
*/
data rndord; set NEW; by id;
seed=974153821;
if first.id=1 then do;
rndno=ranuni(seed);
output;
end;
keep species id rndno;
proc sort data=rndord; by species rndno; /* puts ids in random order */
/* NEW2 will now contain the 8 IDs selected at random */
/*
data new2; set rndord; by species;
if first.species=1 then i=0;
i+1;
if i<9;
proc freq; table species;
/* just to check if, in fact, there are 8 in each */
/* next 3 steps identifies original data by rndno<>. */
proc sort data=new2; by id;
data new3; merge NEW new2; by id;
if rndno<>:;
proc freq; table species; /* to ensure all of the data is there */
/* LEARN will now contain the measurements standardized by size */
data learn; set new3;
array any
NIS_BC NIS_CD NIS_DE NIS_EF NIS_FI NIS_BI
NIS_CE NIS_CL NIS_EL
NIS_BL NIS_FL NIS_KL NIS_LM NIS_IM NIS_AM
NIS_GM;
array any2
DIS_BC DIS_CD DIS_DE DIS_EF DIS_FI DIS_BI
DIS_CE DIS_CL DIS_EL
DIS_BL DIS_FL DIS_KL DIS_LM DIS_IM DIS_AM
DIS_GM;
do over any;
  ANY=ANY/nsize;
if any ne :;
any2=any;
end;
/* TEST0 contains the original data set (not reduced to 10)
so tooth designations go from A-P (for up to 16 teeth) */
data test0; set data.gavredX2;
IF JAW='L' AND SIDE='ORI' AND POSITION='A' THEN GRP='LORIGA';
IF JAW='L' AND SIDE='ORI' AND POSITION='B' THEN GRP='LORIGB';
IF JAW='L' AND SIDE='ORI' AND POSITION='C' THEN GRP='LORIGC';
IF JAW='L' AND SIDE='ORI' AND POSITION='D' THEN GRP='LORIGD';
IF JAW='L' AND SIDE='ORI' AND POSITION='E' THEN GRP='LORIGE';
IF JAW='L' AND SIDE='ORI' AND POSITION='F' THEN GRP='LORIGF';
IF JAW='L' AND SIDE='ORI' AND POSITION='G' THEN GRP='LORIGG';
IF JAW='L' AND SIDE='ORI' AND POSITION='H' THEN GRP='LORIGH';
IF JAW='L' AND SIDE='ORI' AND POSITION='I' THEN GRP='LORIGI';
IF JAW='L' AND SIDE='ORI' AND POSITION='J' THEN GRP='LORIGJ';
IF JAW='L' AND SIDE='ORI' AND POSITION='K' THEN GRP='LORIGK';
IF JAW='L' AND SIDE='ORI' AND POSITION='L' THEN GRP='LORIGL';
IF JAW='L' AND SIDE='ORI' AND POSITION='M' THEN GRP='LORIGM';
IF JAW='L' AND SIDE='ORI' AND POSITION='N' THEN GRP='LORIGN';
IF JAW='L' AND SIDE='ORI' AND POSITION='O' THEN GRP='LORIGO';
IF JAW='L' AND SIDE='ORI' AND POSITION='P' THEN GRP='LORIGP';
IF JAW='L' AND SIDE='MIR' AND POSITION='A' THEN GRP='LMIRA';
IF JAW='L' AND SIDE='MIR' AND POSITION='B'

```

```

THEN GRP='LMIRB';
IF JAW='L' AND SIDE='MIR' AND POSITION='C'
THEN GRP='LMIRC';
IF JAW='L' AND SIDE='MIR' AND POSITION='D'
THEN GRP='LMIRD';
IF JAW='L' AND SIDE='MIR' AND POSITION='E'
THEN GRP='LMIRE';
IF JAW='L' AND SIDE='MIR' AND POSITION='F'
THEN GRP='LMIRF';
IF JAW='L' AND SIDE='MIR' AND POSITION='G'
THEN GRP='LMIRG';
IF JAW='L' AND SIDE='MIR' AND POSITION='H'
THEN GRP='LMIRH';
IF JAW='L' AND SIDE='MIR' AND POSITION='I'
THEN GRP='LMIRI';
IF JAW='L' AND SIDE='MIR' AND POSITION='J'
THEN GRP='LMIRJ';
IF JAW='L' AND SIDE='MIR' AND POSITION='K'
THEN GRP='LMIRK';
IF JAW='L' AND SIDE='MIR' AND POSITION='L'
THEN GRP='LMIRL';
IF JAW='L' AND SIDE='MIR' AND POSITION='M'
THEN GRP='LMIRM';
IF JAW='L' AND SIDE='MIR' AND POSITION='N'
THEN GRP='LMIRN';
IF JAW='L' AND SIDE='MIR' AND POSITION='O'
THEN GRP='LMIRO';
IF JAW='L' AND SIDE='MIR' AND POSITION='P'
THEN GRP='LMIRP';
IF JAW='U' AND SIDE='ORI' AND POSITION='A'
THEN GRP='UORIGA';
IF JAW='U' AND SIDE='ORI' AND POSITION='B'
THEN GRP='UORIGB';
IF JAW='U' AND SIDE='ORI' AND POSITION='C'
THEN GRP='UORIGC';
IF JAW='U' AND SIDE='ORI' AND POSITION='D'
THEN GRP='UORIGD';
IF JAW='U' AND SIDE='ORI' AND POSITION='E'
THEN GRP='UORIGE';
IF JAW='U' AND SIDE='ORI' AND POSITION='F'
THEN GRP='UORIGF';
IF JAW='U' AND SIDE='ORI' AND POSITION='G'
THEN GRP='UORIGG';
IF JAW='U' AND SIDE='ORI' AND POSITION='H'
THEN GRP='UORIGH';
IF JAW='U' AND SIDE='ORI' AND POSITION='I'
THEN GRP='UORIGI';
IF JAW='U' AND SIDE='ORI' AND POSITION='J'
THEN GRP='UORIGJ';
IF JAW='U' AND SIDE='ORI' AND POSITION='K'
THEN GRP='UORIGK';
IF JAW='U' AND SIDE='ORI' AND POSITION='L'
THEN GRP='UORIGL';
IF JAW='U' AND SIDE='ORI' AND POSITION='M'
THEN GRP='UORIGM';
IF JAW='U' AND SIDE='ORI' AND POSITION='N'
THEN GRP='UORIGN';
IF JAW='U' AND SIDE='ORI' AND POSITION='O'
THEN GRP='UORIGO';
IF JAW='U' AND SIDE='ORI' AND POSITION='P'
THEN GRP='UORIGP';
IF JAW='U' AND SIDE='MIR' AND POSITION='A'
THEN GRP='UMIRA';
IF JAW='U' AND SIDE='MIR' AND POSITION='B'
THEN GRP='UMIRB';

```

```

IF JAW='U' AND SIDE='MIR' AND POSITION='C'
THEN GRP='UMIRC';
IF JAW='U' AND SIDE='MIR' AND POSITION='D'
THEN GRP='UMIRD';
IF JAW='U' AND SIDE='MIR' AND POSITION='E'
THEN GRP='UMIRE';
IF JAW='U' AND SIDE='MIR' AND POSITION='F'
THEN GRP='UMIRF';
IF JAW='U' AND SIDE='MIR' AND POSITION='G'
THEN GRP='UMIRG';
IF JAW='U' AND SIDE='MIR' AND POSITION='H'
THEN GRP='UMIRH';
IF JAW='U' AND SIDE='MIR' AND POSITION='I'
THEN GRP='UMIRI';
IF JAW='U' AND SIDE='MIR' AND POSITION='J'
THEN GRP='UMIRJ';
IF JAW='U' AND SIDE='MIR' AND POSITION='K'
THEN GRP='UMIRK';
IF JAW='U' AND SIDE='MIR' AND POSITION='L'
THEN GRP='UMIRL';
IF JAW='U' AND SIDE='MIR' AND POSITION='M'
THEN GRP='UMIRM';
IF JAW='U' AND SIDE='MIR' AND POSITION='N'
THEN GRP='UMIRN';
IF JAW='U' AND SIDE='MIR' AND POSITION='O'
THEN GRP='UMIRO';
IF JAW='U' AND SIDE='MIR' AND POSITION='P'
THEN GRP='UMIRP';
array any
DIS_BC DIS_CD DIS_DE DIS_EF DIS_FI DIS_BI
DIS_CE DIS_CL DIS_EL
DIS_BL DIS_FL DIS_KL DIS_LM DIS_IM DIS_AM
DIS_GM;
do over any;
  ANY=ANY/cSIZE; /* correct to centroid size */
  if any ne .;
end;
proc sort data=test0; by id; /* puts original data in order
of ID */;
data test; merge test0 new2; by id;
/* this associates every ID with a random number if in
learn data set, and missing random number if not—there-
fore only those specimens not included in the LEARN
data set are retained in the TEST data set
if rndno=. */;
/* A discrimination is done using the LEARN data set
with 10 teeth
to create assignment rules based on the 16 measurements;
all teeth
(up to 16 positions) will be assigned to 1 of these 10
positions */
proc discrim data=learn testdata=test pool=yes testout=testo;
title 'DISCRIM BY JAW/POSN/SIDE learn and test
LINEAR';
class GRP;
/* GRP refers to the tooth position, upper, lower, and side
*/
var DIS_BC DIS_CD DIS_DE DIS_EF DIS_FI DIS_BI
DIS_CE DIS_CL DIS_EL
DIS_BL DIS_FL DIS_KL DIS_LM DIS_IM DIS_AM
DIS_GM;
/* TESTO2 will take only those teeth assigned to upper
positions E & F
for further processing and identification of species */

```

```
data testo2; set testo;
if _INTO_='UORIGE' OR _INTO_='UORIGF';
/* go back to the original LEARN data set and select
those teeth from positions D, E, F or G for original uppers
(not mirrors) */
DATA UPERS; SET LEARN;
IF JAW ='U' AND SIDE ='ORIG';
data upper4; set uppers;
if position='D' or position='E' or position='F' or posi-
tion='G';
/* we now use this reduced LEARN data set to assign the
selected teeth from the original discrimination to species.
```

*That is TEST02 will now be assigned to species using the LEARN data set. The results of this analysis then tell us how well this double procedure works */*

```
proc discrim data=UPPER4 testdata=testo2 pool=YES
testout=outDEFG;
class species;
var DIS_BC DIS_CD DIS_DE DIS_EF DIS_FI DIS_BI
DIS_CE DIS_CL DIS_EL
DIS_BL DIS_FL DIS_KL DIS_LM DIS_IM DIS_AM
DIS_GM;
run;
```


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